Ground Beetles (Carabidae) of Fennoscandia

A Zoogeographic Study

Part III
General Analysis With a Discussion on Biogeographic Principles

CARL H. LINDROTH

This is the concluding part of the monographic study *Ground Beetles (Carabidae) of Fennoscandia.*

The book begins with some basic remarks on the prerequisites (material and methods) of zoogeographical research. The author has stated his outlook on these questions more precisely. The somewhat strongly subjective interpretation, in the words of the author, "has the purpose of provoking opposition and open discussion."

The three main sections of the *analytic part* contain a detailed treatment of three special cases, each of which describes one of the three decisive area-limiting factors: the existence requirements of the animal; the dynamic characteristics of the animal; and the influence of time.

The comments in the *synthetic part* are to a large extent based on the results obtained in the *analytic part.* By a combination of conclusions drawn from concrete material of fossil records and somewhat abstract deductions from the present-day distribution pattern of the species the author has attempted to answer the question of the biological significance of quaternary glaciations.

Lindroth's original English summary is reproduced at the end.

Ground Beetles (Carabidae)
of Fennoscandia

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CARL H. LINDROTH

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Rolf Krogerus
Helsinki

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To the Reader

We recommend to follow the instructions given in the "Foreword to this Translation" in Part I of the book.

Manaus/Plön,
July 1988

Joachim Adis
Scientific Editor

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SYNTHETIC PART

PREFACE

7[†] Biogeographical research can be pursued at three different places: in nature, in the laboratory and at the desk.

This series indicates an order of precedence. One cannot escape the fact that the "natural method" not only provides the primary material, knowledge of the area (cf. p. 477; suppl. scient. edit.) of the species concerned, but also direct observations in the field give us first-hand information on the requirements of life for the species and thus offer a clarification of the distributional pattern.

One may go to the desk fresh from the field to tackle the problems, bypassing the laboratory. That has been the way with much biogeographical research, especially in the past. This is quite apart from the fact that in many cases the material was first collated at the desk.

Once I too felt in this way until I gradually realized that the decision as to which factor determines the distribution of a particular species in a given case, cannot be arrived at with fair certainty without experiments. The belief that one may dispense with all experiments is actually a kind of arrogance. Apart from exceptional cases, anyone who can single out the decisive factor right there in nature is truly endowed with extraordinary powers. It is only by experimentation that hypotheses made in the field (or at the desk) can be confirmed or rejected.

The strikingly low reputation that biogeographical research has generally
8 earned in the eyes of other biologists is undoubtedly due to just this regrettable lack of precise methodology and the consequent lack of unambiguous, unprejudiced results. But it is possible to pursue this science more objectively. This means the laboratory must no longer be bypassed.

This concept, which I owe above all to the influence of my friend Rolf Krogerus, has brought me immense relief. The responsibility has been to a great extent lifted from the shoulders of the poor scientist and passed on to the insect, which "answers" the questions through its behavior in various apparatuses. On this is based the relative objectivity of the results achieved, but

[†](Pagination of the original German version to which page citations in the text of this translation are referring to; suppl. scient. edit.)

not just because they can usually be expressed numerically. Modern biology generally shows altogether too strong an inclination to illustrate everything numerically, without always considering how these figures were obtained.

The series of steps (first: study of nature; second: experiments; third: conclusions) recommended here in the work of a zoogeographer suffers from the weakness of all democratically functioning systems due to opposition on the part of workers. Above all, it is cruel not to be permitted to think until one has all the necessary premises to hand. On the contrary, inclination, which is more intuitive than rational, always tempts me to form enthusiastic, bold conclusions as soon as the primary material becomes available, to look for answers when the questions are yet to be properly framed for lack of sufficient premises. Such attempts to take the desk into the field have often proved unsuccessful. It means bringing preconceived ideas to the solution of the problem. How often the subsequent experiments which are "dutifully" executed to confirm the established hypothesis are unexpected and unwelcome! And what self-discipline it takes to junk the beautiful structure and find a new approach to the problem instead of fiddling the data to make them fit!

The present book is thus not the result of a calm, purposeful work. It is on the contrary a heterogeneous mixture of scarcely interrelated questions which, uninvited, clamored for an answer. And the answer was often a compromise between the rival claims of a "heurella" (I've found it!) and a "nitschevo" (never mind!).

However, it is no misfortune when traces of this erratic method of work peep out between the lines. Science is after all not an industry, it is the grand adventure.

Djursholm,
September 1948

Carl H. Lindroth

10†

INTRODUCTION TO PART III

The first two parts of this work, published in 1945, present the material for the general zoogeographical aspects which are dealt with in this concluding part.

This treatment is necessarily both lengthy and to a certain extent one-sided. If the Nordic carabid fauna, in all 362 species, would be considered and discussed under all those aspects of interest for zoogeography, then the present work would cross all bounds. "For the sake of completeness" some sections would have to be included that would be irrelevant to the main issue. But as already pointed out in the Preface to Part I, *this is the postglacial—and possibly the glacial, history of the Fennoscandian fauna.*

As examples of such aspects ignored here or only touched on, however interesting and productive, we may mention: synecological and generally quantitative research, qualitative distribution into ecological groups (p. 35); studies of races and analysis of variations in the material (p. 20); and division of the Fennoscandian territory into zoogeographical regions (p. 43).

Even then the tasks undertaken involved a disquieting tendency to enlarge and refine during the course of the investigation, to the extent that I sometimes despaired on seeing only fragments which defied incorporation in the main body of the text.

So I had to restrict the scope of this work. At the same time, degeneration into a general superficial study had to be avoided. I therefore selected *definite* problems, and hence *definite* species, so as to be able to carry out more detailed studies, in the hope that from the results obtained and the methods developed
11 a broader concept of the conditions for life and the history of the entire Fennoscandian carabid fauna could be developed. In the general arrangement of the text this finds expression in the division of the main part of the book into two, one dealing with *analysis* and the other with *synthesis*. The former contains more original research and more conclusions based on experiments. It turned out to be practical to begin it with the details of experiments. Of course the "synthetic" part also contains references to experiments, but the arrangement of the data at the beginning of the book seemed a good idea because it is more convenient to refer to them there than at the end amid

†(Pagination of the original German version to which page citations in the text of this translation are referring to; suppl. scient. edit.).

the supplement to the first two parts, list of references, index and English summary.

Moreover, the "analytic" part is also an example of *extensive* research. It deals with too many species to delve thoroughly into the physiology of even one of them. But it was not the intention to strive for *precise* values concerning the response of one or other species of animals. The physiological results were only the secondary objective, or more correctly "preliminary objective." They were designed to provide for a more viable *comparison* of the ecological requirements, of the dynamics,† etc. of an entire series of species. I wanted to find out whether the behavior of these species in diverse ways in nature corresponds with various responses to definite and as far as possible isolable factors.

The book begins with "some basic remarks." This is a series of small articles apparently bearing little relation to the main theme. Actually they involve the basic prerequisites (material and methods) for zoogeographical research. I wanted to state my outlook on these questions more precisely, and the somewhat strongly subjective interpretation has the purpose of provoking opposition and open discussion.

The three main sections of the *analytic* part contain a detailed treatment of three special cases, each of which describes one of three decisive area-limiting complexes of factors: the *existence requirements* of the animal (exemplified by the "limestone species"), the *dynamic* ("dispersal-ecological") *characteristics* of the animal (exemplified by the fauna of the islands), and the influences of *time* (exemplified by species exhibiting wing dimorphism).

The comments in the *synthetic* part are to a large extent based on the
12 results obtained in the analytic part. The area-limiting factors are here reviewed in the usual way, with the *present-day* conditions considered first. But it is clear that these are inexplicable without a knowledge or at least an estimation of the *prehistoric* conditions. An attempt must therefore be made to acquaint ourselves with the Fennoscandian fauna of earlier eras. It is best to go backward and to begin with the study of ascertainable changes in the fauna of recent decades. By a combination of conclusions, drawn on the one hand from the concrete material of woefully incomplete fossil records, and on the other hand by more or less abstract deductions from the present-day distribution pattern of the species, it is possible to enter cautiously into the earlier parts of the postglacial period and to approach the central question that this work sets out to answer: *the biological significance of quaternary glaciations*. The objective of this investigation may be considered achieved only to the extent that I have been able to answer this question convincingly.

†(cf. page 13 of this volume and page 15 of Part I; suppl. scient. edit.).

At the end there are four supplementary sections:

1. English summary. Here, only the most important results of Part III are briefly discussed.

2. Supplement to the first two parts. This includes any new records that contribute to the significant improvement of the earlier distribution maps, and confirmations of older or doubtful records. New information on ecology, "biology", dynamics, and fossil records has also been incorporated, and in some cases taxonomic remarks (*Amara communis, Badister bipustulatus*). Only one species new to the area could be added: *Lionychus quadrillum*.

3. List of references. In addition to the literature used in Part III, such further references concerning the first two parts of the book are included as have appeared recently or were omitted earlier.

4. Index to Part III. This includes only the Fennoscandian Carabidae, including the place where each species was recorded.

Finally there are two questions on terminology:

1. The word *postglacial* is used here (as by most biologists) in the widest
13 sense, meaning the entire period since the maximum of the last glaciation. Geologists specializing in the quaternary period, on the other hand, divide this period into the *late glacial* and the *postglacial* (s. str.) periods.

2. Ekman (1922, p. 308) is credited with recognition of two well-defined groups of area-limiting factors affecting an animal or plant species. He calls these *existence ecology* ("Existenzökologie") and *dispersal ecology* ("Ausbreitungsökologie")†. The first of these includes the requirements of life for the animal (or the plant) in its environment and the second concerns its capacity to seek areas suitable for habitation. Corresponding with this we generally speak respectively of existence ecological ("absolute," Reinig, 1938, p. 46) and *dispersal ecological* ("interim," Reinig, l.c.) area limits.

However, these terms are very unwieldy, and the second has the drawback of not being internationally understood and being difficult to translate. The German translation of the good Swedish word "spridnings-ekologi," which clearly expresses the dynamic character of the term, has often been inappropriately rendered "Verbreitungs-Ökologie" (= *distribution ecology*) (for instance, Heinze, 1932–35), although "distribution" indicates a static condition!

In Part I of this book, instead of *dispersal ecology*, I have throughout used the term *dynamics* ("Dynamik"). Here I will use the term *dynamic limits* ("dynamische Grenzen," lignes dynamiques) for dispersal ecological area limits. The existence ecological area limits will be called *existence limits* ("Existenzgrenzen," lignes d'existence); they could also be called *static limits* ("statische Grenzen," lignes statiques). It seems superfluous to drag on the stem "ecology" with these terms.

†(cf. pp. 43 and 203; suppl. scient. edit.).

In the present work the term "ecology" is always understood to denote existence ecology, and the word is generally used in this restricted sense in the literature.

13 # Basic Remarks

On Modern Insect Taxonomy

Contemporary insect taxonomy has three main features:

1. The splitting of genera.
2. The renaming of species.
3. The splitting of species into categories of lower rank (subspecies, "race," variety, form, aberration, etc.).

14 All three features are especially strong in the taxonomy of Lepidoptera. However, they are basically to be considered as modern characteristics related to the entire taxonomic-biological nomenclature, both zoological and botanical. Each of these problems will be considered separately.

1. The process of *splitting the old, large genera*, having simple names, easy to pronounce and remember, into *numerous, less comprehensive genera*, has been carried to extremes in the family Noctuidae. Momentarily even the experienced specialist in this field may not know the genus to which one or other species, otherwise familiar to him, belongs. The result may be heard in any conversation between lepidopterologists: they consistently use only the species name for their favorite insects. Any one wishing to describe a new species of Noctuidae looks for a name that is new not only in the genus but also in the family, and if possible in the entire order Lepidoptera. *The splitting of genera has actually led to the end of the binomial nomenclature.*

Instances of such splitting of old genera, disastrous from the practical viewpoint, are also found in other insect orders. Clear evidence is to be found in the new, otherwise exemplary, revision of the Nordic species of *Cicadina* by Ossiannilsson (1946–47), and in the otherwise perfect monograph on Coleoptera, unfortunately not completed, concerning the Palaearctic Ceuthorrhynchinae by Hans Wagner (1938, p. 172).

But coleopterologists have at least generally been more prudent. In the systematics of Carabidae specialists like G. Müller and Schauberger have even merged some of the generic entities, earlier considered separate, into the genus *Agonum* and *Harpalus*. Jeannel (1941–42) has, on the contrary, taken the opposite course, and has split all the larger carabid genera. For instance, *Bembidion* has been split into 17 genera!

If the procedure adopted by Jeannel were to serve as a model for carabidologists—which I certainly do not anticipate—it would signify a great loss, the loss of familiar generic names which we have used for many generations as tags for these animals. It is of course correct that the higher taxonomic categories (genus, family, etc.) should, wherever possible, reflect
15 the true *relationship* (i.e. common origin) of the animals. But this is only *one* of its functions, and it is best not to insist on it too strongly. It seems it is no longer possible to take bold, categorical decisions as to what is "primitive" and what is "derived" in the organization of an animal. If such considerations alone were to serve as the guiding principles for monographers, then very soon every author would have his own "system."

The *other* aspect of taxonomy is purely *practical*. The special purpose of the generic name is to give the nonspecialist an indication as to where the species in question belongs. In a zoogeographical, ecological or physiological study, etc. it would be very undesirable if every time a species was introduced into the discussion it was necessary to give its systematic position just because its name was known only to taxonomic specialists. *The primary task of the systematist is to give the animals easily understandable and, as far as possible, stable names that can be utilized by the main body of biologists the world over. The idea is not to provide themselves with counters for playing the adventurous game of phylogeny.* In terms of nomenclature this branch of biological research has been adequately endowed with the erection of subgenera or species-groups, whose names need not be used when the animal is mentioned in non-phylogenetic contexts.

From the viewpoint of a practical nomenclature *the genera are better too large than too small.* It is no misfortune if the isolated species-groups which might merit the rank of a genus (among the Carabidae for instance, *Europhilus* or *Ophonus*) are maintained as subgenera (also compare Handlirsch, 1913a, p. 71). With regard to the generic names which were changed as a result of application of the rules of priority, see below.

2. The entire realm of zoology and botany of the last century is marked by an extensive *change of species names*, a trend that has increased rather than decreased during recent decades. Thus we find that in the Fennoscandian carabid fauna, since Grill (1896) 35 species (11%) have been given new names, and this of course excludes species which were simply misidentified or were
16 later split. Going still farther back to Thomson (1885), the number increases to 77 species (28%). Even since the publication of the Nordic Catalogue (1939) six names have been changed. If all the "new" names used by Csiki (1927–33) and Jeannel (1941–42) were accepted the number of name changes would further increase. The same is substantially true of the generic names.

The chronic instability is evidently undesirable. Is it necessary?

Some of the name changes are unavoidable. Wrong identifications must be corrected (for example, *Bembidion scandicum* as against *B. macropterum*). Besides, more careful modern studies have shown that some of the earlier species

must be split (for example: *Notiophilus "palustris"* and *Harpalus "luteicornis"* of early authors).

But this is not true of the majority of cases. On the other hand, there are cases where, probably by the study of a specimen named as the type by an earlier author, it becomes clear that the name he gave has subsequently been used for a different insect. Or, more often, rediscovered works reveal a name which is ingeniously ascribed to a species now known generally by a *more recent* name. Most of the mischief is due to the "law of priority" (Règles Internat., 1905; Handlirsch, 1913b).

A clear instance in the systematics of carabids is the case of *Harpalus* (*Ophonus*) *"brevicollis"* and *"rufibarbis,"* which I have discussed earlier (1943, p. 25). Each of these names has been used at various times either for *seladon* Schaub. or for *schaubergerianus* Puel. Hence it seems inappropriate to retain any of them.

Another kind of example is that of *Nebria gyllenhali* Schönherr (1806), whose name Jeannel (1937) sought to change to *rufescens* Ström (1768). Yet the former name has been in use almost as the only name for more than a century in Europe, despite the fact that *rufescens* was undoubtedly proposed as a modification of forma *rufino*, and was named after it (see Lindroth, 1939b, p. 59). Why does Jeannel wish to follow the law of priority most rigidly in this case, whereas in the case of *Abax ater* Villers (1789) he (1941–42, p. 776)
17 refuses to replace it by *parallelepipedus* Piller & Mitterpacher (1783), among other reasons, because "l'espèce est bien connue sous son nom d'*ater* Vill."?

No wonder the consequences of the rigid application of the law of priority have aroused serious misgivings and clear opposition from the most level-headed entomologists. Heikertinger, particularly, champions the opposite view. In a long series of articles* (see list of references at the end of this book), he adduces a wealth of evidence *in favor of the principle of continuity as against the principle of priority.*

The principle of continuity is emphasized in the following declaration (and also Heikertinger, 1935, pp. 147–148; 1939a, p. 221; 1942a, p. 26; 1942b, p. 1):

"The valid name of a genus or species is that found in use in the scientific literature, whether or not it was given first. If there are two names in use for a genus or species, then the revisor should choose the name whose retention will produce the fewest nomenclatural changes in the existing literature."

These views represent a true anarchy against the principle of priority. Must they prevail in order to prevent the continuation or even accentuation of the present intolerable situation? Or are more moderate solutions possible, which may satisfy the "priority people," at the same time ensuring nomenclatural stability? Heikertinger (i.e. 1939b, p. 561) suggested such a compromise.

*Heikertinger's article of 1942b includes a complete list of his papers on nomenclatural problems.

One idea is the "limitation proposition," i.e. species and genus names that have been the only ones in use for a definite number of years (Horn, 1938, p. 2, suggests 20 years) should not be changed.

A second suggestion is "*nomina conservanda*," i.e. a list of names of animals should be prepared that must not be changed in future under any circumstances.

In this way, one has attempted to save from destruction at least some of the most commonly used scientific names of animals, and of course among insects primarily those related to applied entomology. Escherich (1940) has
18 suggested the preparation of a long list of *nomina conservanda*, which should primarily include the economically most important insects. But Heikertinger (for instance, 1941, p. 230) has rightly pointed out that systematics cannot be helped with such lists. On which principles are certain names to be selected for the list? How could agreement on these be achieved among specialists, in Commissions and at Congresses? How much time and how much paper would be required for selecting the "deserving" names from among hundreds of thousands! Finally, if a *nomina conservanda* list would be prepared on such a large scale and one (really?) assumes that it represented a definite advantage for taxonomic research, then the names would no longer be "exceptions" to the rules of priority. The rules could as well be suspended and all such names as are currently valid, declared "conserved."

If after the above reasoning I still have definite reservations about the unconditional acceptance of Heikertinger's "principle of continuity" it is mainly on account of the possible abuse of the expression "the most frequently used names." It cannot be expected that every zoological systematist, not even every distinguished specialist, would strive to undertake a really objective investigation in doubtful cases as to which of the names of a genus or a species are "currently" used most frequently. I am afraid the decision would generally favor one's own geographical or linguistic region, for instance, the Americans would tend to conserve their own names. I indeed concur with Horn (1938, p. 2) when he says: "It would be no misfortune if temporarily here and there two or three names were considered valid at the same time (i.e. in different countries) for the same insect form." It would probably not be a misfortune, but a great inconvenience which would lead to many misunderstandings. It is all the more so since the word "temporarily" used by Horn seems to be rather too optimistic.

If the simultaneous use of two or more names for the same species of animal (or genus) poses only a possible inconvenience, then the gloomy word "misfortune" is appropriate for the converse situation, i.e. *where the same name is used for more than one species of animals*. This would not only make the work of the researcher more laborious but for long periods it would be impossible for him to decide which species was involved at one or other place in the literature, and detailed studies on ecology, physiology, etc. might become nearly worthless.

19 It therefore seems to me that *one of the most important tasks of the Rules of Nomenclature is to prevent the transfer of a name from one species of animals (genus, subspecies, etc.) to another.* Where no synonymic names exist it is better to give an entirely new name if necessary. A proposal to this effect was made at the Zoological Congress in Monaco (1913), but was frustrated by "compromises."

Secondly, I would like to concur with the "limitation proposition" mentioned above. Perhaps it would be appropriate to declare definite "limiting years," somewhat as follows: "Names of genera and species appearing before 1850 and not used in scientific literature after 1900 (or used only as synonyms) must not supersede a name used later." The period would be better shortened than protracted.

The above proposals might be considered as a compromise between the principles of continuity and priority. Nevertheless, I would approve the first without the least reservation, if only I could share Heikertinger's confidence that enough systematists could be won over. However, gentlemen with a penchant for systematics are usually constitutionally conservative and less open to purely practical proposals. I believe they would generally submit only to the decisions or recommendations of entomological or zoological congresses and similar bodies. And many of those who were undecided would prefer to follow the law of priority as "safer."

There is another reason to annul the laws of priority in its rigid form. Changes in the names of species, "name-hunting," is usually the result of digging out older, long-forgotten descriptions. Now these descriptions are almost without exception so trivial that the species in question could be identified simply and solely by a study of the so-called "Type" unless the secondary characteristics of the animal were involved (geographical distribution, biological evidence, etc.). These "type-specimens" of the earlier entomologists—which could often be selected only as the most probable representatives—are now preserved largely in public museums and are not loaned out in some cases (for
20 example, by the British Museum). If the specialist cannot visit that museum he has to depend on second-hand descriptions and comparisons by someone else, photographs, etc. Preparation of genitalia and other structures, which are often essential, sometimes is not permitted by the museum directors. Worse, in the meantime many of these types have been destroyed during the Second World War, especially in Germany, and the political situation scarcely augurs a lasting peace. "Types" are even less enduring than books. To base the nomenclature largely on the former is highly impracticable. The scientific description of an animal, which cannot be interpreted without examination of the type, would be better not undertaken. The principle of continuity or limitation would do away with this exaggerated cult of types (Handlirsch, 1913b, pp. 88–89) and would leave the museums for more important matters.

At any rate the rigid laws of priority in their present form must be set

aside, so that the zoological and botanical literature can free itself from the ban of this "end in itself."

3. Detailed studies on the variability of species—both in animals and plants—have shown that they are less homogeneous than originally believed. In many cases splitting into several taxa of a lower systematic rank has resulted, representing minor requirements upon characters which separate species. In other cases the demarcations between two or more species recognized earlier proved to be so diffuse that it seemed appropriate to merge them—if necessary into "Rassenkreise"* or "Formenkreise"** (Rensch, 1929).

Even where the species constantly manifested its individuality vis-à-vis other members of the same genus, fairly large and more or less stable differences were always found between individuals, groups of individuals (populations), or larger entities. This led to the proposal of a fairly large number of names *within* the species concept.

These categories have been named very diversely. But the one immediately below the rank of a species is universally known as *subspecies* ("Unterart," race). The general requirement is that every subspecies be separated *geograph-*
22 *ically* from others within the same species (for example, Rensch, 1929, 11). In keeping with this, new subspecies are frequently described almost exclusively on the basis of their more or less isolated geographical occurrence.

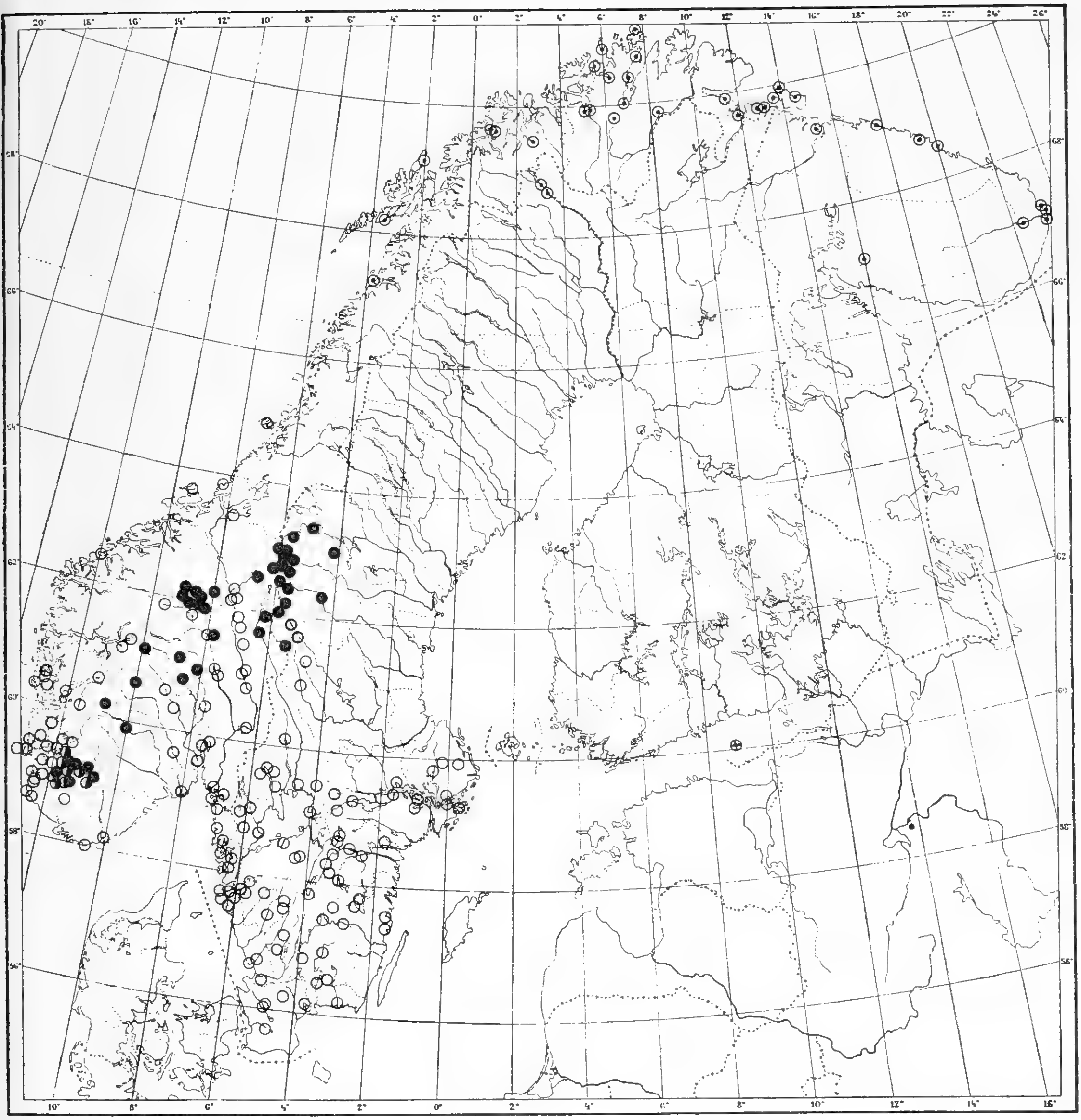
The unsatisfactory result of this criterion is evident from the case of *Carabus problematicus* in Fennoscandia (Strand, 1935). There are three main types of the species found here (Fig. 1) which, if "pure," positively deserve equal rank. One of these (*strandi*) lives geographically quite isolated in the far North and hence fulfills the strictest requirements for subspecies rank. The other two (*wockei* and *scandinavicus*) occur in many regions† of central Scandinavia so close together that at some places (particularly in southwestern Norway) the ranges of the two overlap. There they evidently hybridize, since truly intermediate forms are not exceptional in these zones of intermixing. The original status of *wockei* as a montane form and that of *scandinavicus* as one inhabiting the plains is not strictly maintained here and a geographical line of demarcation between the two forms can no longer be drawn. But there is no doubt that both *wockei* and *strandi* survived the last glaciation within the region, whereas *scandinavicus* represents a race that has immigrated during the postglacial period. A different nomenclatural consideration of *wockei* and *strandi* would therefore be absurd. In the usual systematic categorization these three are to be treated as subspecies.

Assuming that to qualify as a subspecies it is essential that a group of individuals be isolated from other members of the species, it must be realized that isolation can be due to other factors. These include altered ecology, food

*(Polytypic species; suppl. gen. edit.).

**(A collective category of allopatric subspecies or species; suppl. gen. edit.).

†(cf. p. 822; suppl. scient. edit.).



21 Fig. 1. *Carabus problematicus.* The Fennoscandian races.

Plain circles—*scandinavicus* Born.; Spotted circles—*strandi* Born.; Black circles—*wockei* Born.; Crossed circles—"*relictus* Hellèn." Black and white circles—intermediates between *wockei* and *scandinavicus* forms (in south-western Norway).

biology, sensory physiology, etc., thus *geographical* isolation must not be considered as the essential prerequisite for a particular systematic category (cf. Huxley, 1940, p. 27 ff.).

It would also probably be incorrect to want to deny subspecies rank to the two forms of *Calathus mollis* (see Supplement), just because they coexist on Bornholm, and certainly in northern Germany too (according to data in Gersdorf, 1937, pp. 81–82).

The situation in the case of the chrysomelid *Galerucella nymphaeae* L. is still more questionable, since the two forms *nymphaeae* s. str. and *sagittariae* Gyll., rightly considered as subspecies by Palmén (1945), largely occupy common areas. But they seem to be constantly associated with different food plants, and attention could be drawn to the isolating factor by the designation "subspecies *trophica*."

The generally advanced criterion for a subspecies, as the capacity to breed
23 with other subspecies of the same species, although to a "limited" extent, is a quite ambiguous definition and cannot be used in practice.

It is in any case clear that the correct delimitation of a *subspecies* is far more difficult than the description of a new *species*. The characteristics of a species, according to its definition, have a higher degree of constancy (among insects, for instance, often manifested by distinctly marked characters of the genitalia) whereas species that can be divided into subspecies are almost without exception characterized by a strong general variability of minute characters. If it sometimes appears rather adventurous to describe a new *species* on the basis of a single specimen, a little consideration shows that such a procedure is quite unscientific when followed for a new *subspecies*. For the subspecies can hardly ever be defined by clearly marked characters, but only by the amplitude of variation around certain mean values. And to establish that, particularly *extensive material* is necessary.

But such discretion in characterizing new subspecies is not always exercised, at least by the lepidopterists. Bryk (1942, p. 5) may be mentioned as a typical example: "In describing new species I proceeded from the irrefutable postulate that every form of a species already divided into subspecies must belong either to a known subspecies or to a subspecies to be newly recognized and described... In having before me *one specimen* [emphasis mine] which deviates from the known species the question arises, even if it might be an aberration, whether the specimen belongs to a new subspecies or might be referred to one already known. If yes, the specimen undoubtedly represents an individual of a new subspecies."—The more meager the material, the more numerous the subspecies!

It would be a kindness if the specialists would try to confine the characterization of new subspecies exclusively to very clear cases.

The lower categories are of course poorly, often subjectively, separated from subspecies. There is a whole series of terms of higher and lower or-

der, which sometimes seem to be merged (possibly including the subspecies category) under the term "*var.*" (varietas, variety, variant).

An example of an exhaustive and extremely consistent subdivision of the species is provided by the monograph of the large genus *Carabus* by Breuning
24 (1932–36). He follows Semenov (1910; see also Handlirsch, 1913a, pp. 68 ff.) and uses, in descending order, the terms subspecies, natio, morph and aberration (= individual variants, which usually do not deserve a name). This imposing work offers a much-needed remedy for the confusion of names in this genus, where the most insignificant individual color variations have been solemnly named and described by ambitious "researchers." But Breuning's system is rigid and completely unnatural.

This is especially evident from the detailed studies carried out on the morphology and physiology of *Carabus nemoralis* by Krumbiegel (1932). As is very characteristic of a taxonomist of the "old school," Breuning (l.c., p. 665) cites this work without utilizing it in systematics. Krumbiegel has most clearly shown that *C. nemoralis* exhibits gradual morphological and physiological changes (at least some of which are heritable), from the northeast (eastern Germany) to the southwest (southern France), which coincide with the change from a nocturnal to a diurnal life. Krumbiegel provided a good example of a *cline* ("Klin") even before the term was proposed.

The enormous advantage of the concept of *cline*, formulated by Huxley (1939), is that one must precisely determine and trace out the gradation *of every single variable character* within the area of the species. According to Huxley (for example, 1945, p. 226) the *cline* method in no way replaces the division into subspecies. On the other hand there is no doubt that its consistent application to a strikingly variable species would demonstrate that some (I should like to say *most*) of the subspecies described so far are untenable.

It is deplorable that Petersen (1947), the first-ever entomologist (and the only zoologist) to analyze variations by the *cline* method in the Fennoscandian Region, in his studies on certain widely distributed butterflies not only largely retains the older subspecies but also describes new ones, some of which are very poorly delineated.

Certain carabids of the Fennoscandian Region may also be considered suitable subjects for future research by the *cline* method. One might mention *Carabus glabratus, C. violaceus*, and *Cychrus caraboides*, in which, among
25 others, the following characters may be considered: body size, comparative length of pronotum: elytra, length index of pronotum: width, curvature and surface (microsculpture) of elytra; in *violaceus*, also the color; in *Cychrus* the shape of the posterior angles of the pronotum and the proportions of the legs (especially the hind legs). In the welter of confusion in the Central European *violaceus-purpurascens* complex some degree of order can be brought about only in this way.

The lowest systematic entities, wherever possible, should be denoted only

by code words ("Kennworte") (such as f. *nigrino*, f. *coerulescens*, f. *impunctata*, f. *rufipes*, etc.) *without the names of authors*. Otherwise they are best left unnamed (as in Lepidoptera, suggested among others by Kiriakoff, 1948). Naming of aberrations is useful only if the nature of the characters as a modification or a mutation has been determined, in this case the expressions "f. *mod.*" or "f. *mut.*" may be used. The wing dimorphism dealt with in this book shows that even a strong morphological as well as a physiological modification can be due to the influence of a single gene.

With the exception of the cases mentioned above, members of the Fennoscandian fauna of Carabidae are unusually homogeneous, since they show very little regional variation within the region. Therefore little attention has been paid to this aspect in the present work, nor is there a special chapter devoted to this problem.

The reason for this uniformity in the fauna is undoubtedly the infancy of the fauna, as well as the extensive enlargements of its area during the later post-glacial period (< 16,000 years), which have been of the nature of enormous and incessant intermixing of populations. Nevertheless the stocks which remained isolated along the Norwegian coast during the Würm glaciation, of which numerous examples are given below, show a tendency to form subspecies only in exceptional cases (*Carabus problematicus*). Thus normally the formation of new systematic entities, even of a lesser rank than species, requires longer periods of time than is generally assumed (Lindroth, 1941, p. 437 ff.).

Among aberrations in Fennoscandian Carabidae the following might be mentioned: all gradations of *nigrino* and *rufino* forms, the former of these predominating in *Calathus melanocephalus*, the latter being especially marked in *Amara alpina, A. torrida, Bembidion prasinum, Nebria gyllenhali, Patrobus septentrionis, Pelophila*. In my opinion both of these represent modifications.

26 On the other hand the black- or red-legged character of some species is probably genetically determined, for instance in *Anisodactylus binotatus, Calathus fuscipes, Chalaenius nigricornis, Harpalus aeneus, H. fuliginosus, Nebria gyllenhali* (*balbii*), *Pterostichus cupreus*. Of these, the red-legged *Nebria gyllenhali balbii* alone is regionally restricted. —The color is especially variable in most of the metallic species, chiefly *Harpalus aeneus*.

Distinct pairs of subspecies are found only in *Badister bipustulatus, Calathus mollis, Carabus cancellatus*, and *Patrobus septentrionis*. In all these cases there is an eastern and a western subspecies, which partly coexist only in the case of *Badister* and *Calathus*. Some very closely interrelated pairs of species, such as *Amara cursitans* and *municipalis, Badister dorsiger* and *sodalis*, might possibly represent subspecies. The status of the "subspecies *silvicola*" of *Amara quenseli* is doubtful.

On the Consideration of Literature

The volumes of the *Zoological Record* of recent decades placed side by side convey an idea of the relative output each year in zoology. The inhibiting effect of the two world wars is all too evident. Still, during the 20th century there has been a sharp increase in the zoological literature. This growth has been especially marked in entomology.

The unavoidable consequence is that every careful researcher must sacrifice much time to the study of the literature in his field. This burden has become so great that the question arises whether this time could not be better spent.

Some authors go all out for a "complete" list of references in their particular field almost as a sport. It is all the more annoying when at a Swedish inaugural dissertation the opponent puts it to the poor respondent that he has "forgotten" a certain reference, regardless of whether this would have had a vital bearing on the theme.

As long as the zoologist or botanist, as a specialized systematist, works within the confines of a well-demarcated group of animals or plants, the
27 requirement of knowledge of all the literature, if possible, in that particular field is justified. The specialist must not only be familiar with the animals but must also be aware of the views published by other authors on the systematic position of every species, genus, etc. Otherwise many statements contradicting each other will frequently remain uncontested, which would result in confusion.

A good example among carabidologists is provided by Jeannel, author of the exemplary monograph on Trechinae (1926–28). When he later turned to other carabids, in order finally to revise the entire family in *Faune de France* (1941–42), for unknown reasons he largely ignored the literature. This naturally resulted in completely unnecessary mistakes and misunderstandings. In particular, his data on the total area of each species are frequently misleading because they are incomplete.

On the other hand, the reverential consideration of the literature can be overdone, even by a specialist. Especially among phytogeographers, for every species treated a detailed report is often provided on the history of its discovery in the region, including all the literature (for instance, Degelius, 1935). Although it reveals an interesting part of the history this method seems inadvisable to me. It tends to enlarge the scope of a biogeographical monograph beyond reasonable limits, without adding to the material content.

The situation is somewhat different in the fields of physiology, ecology, zoogeography, etc. Here a knowledge of the animals studied is not an end in itself, but the material under study is to be used as a basis for conclusions with general validity or at least a validity beyond the scope of the material. Conversely, the results obtained by other researchers on other animals can

naturally be of great significance in such a study. The question is: To what extent is one obliged to take such literature into consideration?

The zoogeographer is in an especially difficult position when he requires information from the auxiliary sciences like general geography (even cultural geography), geology, climatology, also often soil chemistry, the theory of heat in physics, even archaeology, etc. Besides, he must always keep an
28 eye on the experience gained by botanists. In these fields he is usually a complete novice who must rely on the literature or on statements by other experts.

My personal opinion concerning study of the literature by a zoogeographer is as follows: He must thoroughly acquaint himself with the *primary material.* He should put together as much data as possible on the taxonomy, distribution, ecology, etc. of the animals concerned, and spare no pains to completely gather this information from the literature, the museums, or private individuals. Such data form the basis of the first two parts of this book.

Next follows the *collation* of the primary material, the endeavor to answer all the questions that arise during this compilation, and those characterizing the complicated problem of every species: How has the area taken its present shape?

A judgment can be arrived at by two methods. Either one can look for many, perhaps similar, cases and problems in the literature and check the experience of other researchers against the case at hand. Or, one can treat it as an isolated problem using observations in nature, experiments and wholesome "farmer's sense," without prejudging the issue.

Although in general perhaps a combination of the two methods seems desirable I decidedly prefer the latter. This choice is not one of convenience, and it must not be judged as an expression of haughtiness ("Hybris"). But as far as I can decide, a thorough knowledge of the *case* in hand is more important than of the *method* used by other researchers. Finally, I did not have enough time to go through the relevant literature on zoogeography, phytogeography, ecology, physiology, etc., and I am convinced that such a study would have deprived the working task of much of its liveliness. After all, the method adopted is therefore an expression of personal preference.

This is my defense against the reproach, certainly justified in some cases, that I have not sufficiently taken the literature into consideration. I have utilized such works as I have often come across accidentally that might contribute to a solution of the problems posed. A complete historical review of a particular branch of research has never been achieved.

On the contrary, I would like to assert that it is often useful to re-
29 searchers concerned with the general problems of ecology, physiology, etc., to go more deeply into the elementary characteristics of the objects of their investigation. By this I mean that such investigations should be preceded by a thorough knowledge of the taxonomy, biology (in the broader sense) and

distribution of the species of animals concerned; but this is not always the case.

On the Task of the Museums

The public and private collections of natural history specimens had their beginning as showcases containing objects of curiosity. As descriptions of the animals began to appear in print from the 18th century and they were classified into a system, they ceased to share the status of philately, yet the collections largely remained at that level to this day.

In the meantime, the requirements of entomological researchers, especially in the fields of zoogeography and ecology, have also greatly added to the tasks of public museums and hence created more difficulties for them.

To get an idea of the extent to which the larger museums can satisfy such modern requirements, and of what improvements seem to be especially desirable, I have made a compilation of the existing conditions mainly through enquiries addressed to the curators of leading museums of the Nordic countries.

The curators of museums who answered all of my enquiries in detail, for which I sincerely thank them here, were:

Zoological Institute of the University of Lund† (*ML*). Lecturer Kj. Ander.
Zoological Museum of the University of Oslo† (*ML*). Dr. L.R. Natvig.
Zoological Museum of the University of Helsinki† (*"Helsingfors"*; *MH*). Dr. R. Frey.
Zoological Museum of the University of Åbo† (*MÅ*). Professor K.J. Valle.
Zoological Museum of the University of Copenhagen (*"Kobenhavn"*; *MC*). Dr. S.L. Tuxen.

Through my own experience I was sufficiently acquainted with the entomological collections of the *Natural History Riksmuseum, Stockholm* (RM; Director Professor O. Lundblad) and the *Natural History Museum, Göteborg** (MG; Director Fil. lic. H. Lohmander).

For the sake of clarity the result of the enquiries is presented here in the form of 10 questions, which were directed to the museums concerned, and in each case some remarks have been added.

It was assumed that each museum was concerned with *the fauna of its own country*, which is actually the case at present in all the museums mentioned.

The following summary takes into account only the collections of *Coleoptera*, but in principle might be relevant to other orders of insects.

1. Has all the indigenous material been brought together into a single

†(cf. pages 19, 21, 22 of Part I; suppl. scient. edit.).

*In MG, for lack of staff, so far only Carabidae, Heteromera, and Longicornia have been provisionally put together.

collection? (see also question 6!). Or are there also special collections which are maintained separately for reasons of reverence, as voucher material of certain publications, as special geographical collections, etc.?

The answers revealed that all the museums mentioned have tried to avoid, so far as possible, any distribution of the indigenous material among several collections. In some cases donations of material were even refused because of the condition attached that the collection must be maintained separately.

However, in the museums mentioned, with the exception only of MO and MÅ, besides the main indigenous collection the following special collections of Coleoptera are present:

a. For reasons of reverence: coll. Boheman in RM: coll. Roth in ML; coll. I.B. Ericson in MG.

b. As voucher material of scientific publications (partly also acquired private collection): coll. Zetterstedt ("Insecta Lapponica") and coll. Thomson in ML; coll. Lindroth (only carabids) in MG; coll. Mannerheim (world collection) in MH; coll. Schiødte in MG.

c. Special geographical collections are maintained only in RM from the nature reserves of Gotska Sandön as well as Sarek and Abisko in Lapland.

d. In addition, all museums connected with universities have special reference collections which are not taken into account below.

31 Horn (Horn and Kahle, 1935–37, p. 497) has listed reasons why the separate arrangement of a collection may be justified. "Reasons of reverence" is not one of them. It does not seem to be justified to maintain separately the above-mentioned collections of Boheman, I.B. Ericson, and Roth, since their owners published comparatively little on the indigenous Coleoptera, and the collections can scarcely serve as voucher material. The present curator of ML is of the same opinion.

On the other hand, the four collections mentioned in par. "b" above, brought together by leading entomologists of their time, are historically valuable. Even the unlabeled insects among them, which would be put away as a result of merging with the main collection, are valuable as voucher specimens for the opinions of the respective authors.

The Zetterstedt collection may also be considered a special geographical collection. Such collections are otherwise present only in RM, where the curator also seems to be inclined to discontinue their separate maintenance. But in my view special geographical collections, for instance of islands or regions that have recently undergone big changes as a result, say, of damming operations, are very important for entomologists working with zoogeographical problems. So are special ecological collections, for instance from sampling areas where an exact inventory of the fauna has been realized. I would prefer to see an increase rather than a decline in this practice.

2. Has a certain maximum number of specimens been laid down for every

species in the main collection? What is generally done with new material that does not earn a place in the existing box for the species?

The answers show that at present a limit on the number of specimens is imposed only in RM and MÅ, in the former case according to provinces (see question 3), and in Åbo (for the time being) restricted to 20 (–40) specimens of each species.

3. Are specimens of every species arranged geographically? If so, is there a limit on the number of specimens from each province?

All the answers expressed the desirability of having a geographical arrangement of the material. But in MG, MO, and MC it had to be dispensed with for lack of staff.

A consistent limit on the number of specimens from each province is followed only in RM, where it is "half a transverse row" (=3–4 pins, each row often with several insects).

32 4. Is each province represented by as many localities as possible? Or if the space assigned to the province has been filled up, are any specimens coming in later considered duplicates?

All but one of the museums try (probably within limits due to lack of space), to acquire representative specimens from as many localities as possible. The exception is RM where a full "half-transverse row" in the box means no more specimens from the province are to be incorporated in the main collection, even if all the specimens already present originate from a single locality. This procedure is in no way consistent with the present-day requirements of a geographical collection.

5. What is to be done with large series from the same locality?

In MO the maximum number of specimens from every locality is fixed at six. Other restrictions are evident from the answers to questions nos. 2 through 4. Only MG, MH and MC try to maintain a large undivided series.

6. Is there a special collection of duplicates, that can be utilized for exchange or donation?

There is in RM, MO, and MÅ. In MG, ML, MH, and MC *all the material* is maintained in the main collection (at least for the time being), or some of it is temporarily kept in supplementary boxes.

An answer especially congenial to me was given by S.L. Tuxen (MC): "*The term of "duplicate" simply does not exist*!"

7. Must all the material be uniformly prepared? Or is there a perfectly prepared special "systematic" main collection, while the "geographical" collection is more heterogeneous?

Only in RM does the curator insist on perfectly mounted material (on rectangles) for the large (geographical) main collection, established about 15 years ago. Some of the "better" older insects are remounted for this purpose. All the other curators of museums entirely discount a uniformly prepared main collection.

33 None of the museums has separated the "systematic" from the "geographical" collection, but Kj. Ander (ML) considers such a distinction desirable.

8. Must specimens be "perfect"? What is done with defective specimens?

All but one of the curators replied that "perfection" counts only in the sense that highly defective specimens are replaced by better ones (from the same locality or at least from the same province). The exception is RM where, with the exception of very rare species, a defective specimen is not included in the main collection if as little as an antenna or tarsal segment is missing.

It can be said that such an attitude to a *geographical* collection is quite unscientific. An identifiable fragment from a distant locality is far more interesting than any "show-piece" from an insignificant region. The most far-sighted definition of the term "defective," even from the viewpoint of the systematic entomologist, was given by Ganglbauer (Heikertinger, 1914, p. 137): "So long as a specimen possesses one complete antenna and three different legs undamaged it is not defective."

9. Has the attempt been made to achieve uniformity in the contents and design of the locality label? How is the indication of the collector's diaries given, if they exist?

In all the museums at present the collector's original locality labels have been retained (if they exist), which is undoubtedly correct. If these labels are much abbreviated or badly written, occasionally a more detailed printed label is attached, at least in ML. It would be welcome if this procedure was adopted more commonly for indistinctly labeled, especially older material.

To date the exemplary practice of affixing a register number ("Journal-Number") to every insect is followed as a rule only in Finland. General compliance would be highly desirable. In this case, it is furthermore important that the museum acquires a complete copy of the daily diary of the collector. This has been the case with MH since about 1850.

10. What is the procedure for maintenance of genitalia and other preparations, larvae and pupae preserved in liquid, pieces of food, etc. relating to a species or a specimen of the pinned collection?

34 I was informed by ML and MÅ that genitalia preparations, wherever possible, are attached to the pinned insects on a strip. If film or similar material is used, preparations in Canada balsam, etc. can also be affixed in this way. Separately maintained preparations are indicated by definite numbered labels in all museums. It is recommended that for such labels colored paper indicating the particular collection be used.

The above exposition is a survey of the principles at present followed with regard to the indigenous collections of our museums. In various remarks my own views on these questions may have found expression to some extent. However, I will here briefly recapitulate them more precisely.

All accurately and reliably labeled material is valuable. There are no "duplicates." Identical stamps do exist but not identical animals. It is therefore insufficient to strive for representative specimens from as many localities as possible; the museums must maintain large *series* of animals collected at the same time. The present work clearly shows, in the treatment of carabids with wing dimorphism, how important the presence of larger series can be. Certainly in the future, when according to all indications, pure systematics will also get involved in analysis of variation, the need for quantitative completeness of material will be more and more urgent.

The objection that the museums have neither space nor time (i.e. staff) for this can be met in the first place by the argument that less important pursuits should be restricted! As soon as more reasonable conditions with regard to entomological nomenclature are achieved, the decline in the type-cult on the part of museum officials will save many valuable working hours. Also the mistaken pretension of some museums of being in possession of a Palaearctic or even world collection, deprives them of much energy. If every museum accepts as its main task the maintenance and compilation of the *indigenous fauna* it will be possible to treat this collection according to modern concepts. This does not mean that special collections of another kind (for instance, material collected from foreign countries or world collections of smaller systematic groups, which have been acquired incidentally by donation, exchange, profitable purchase, etc. or as a result of foreign expeditions by local researchers), must be neglected.

From the purely practical viewpoint the indigenous collection must be arranged in such a way that supplementary boxes can everywhere be fitted in and all the boxes replaced without any problem. It is impossible, even after the establishment of large geographical collections, to estimate how much space a species will require after 50 or 100 years. It is impracticable to put all the specimens that cannot be accommodated in the proper boxes in a special supplementary cabinet. It may be said that such an enormous collection with hundreds of specimens of almost every species must be difficult to survey. It is, for the usual systematic purpose, i.e. identification. I am inclined to favor the solution given above, that besides the large *main geographical collection* an indigenous *main systematic collection* be maintained. In this, normally two pairs of every species (several specimens of variable species) would be preserved, all mounted perfectly and "flawlessly" and provided with the necessary genitalia or other preparations and "authoritative" determination labels*. This collection should also contain all the uniques, which would be indicated in the geographical collection where appropriate by a small label.

On the whole I am no opponent of special collections of the kind indicated

*In general the museums should strive to supply a determination label with every animal *bearing the name of the determinator.*

above (Point 1). But it is also appropriate that if a species is not represented in the geographical collection from the province concerned, an indication on a small colored label be provided referring to the special collection. If such indications are consistently entered in the geographical collection, along with information on genitalia preparations (when separately preserved), any larval collection, pieces of food, etc., this will serve as a kind of central card index, making it unnecessary to organize a special card index.

On Synecology and "Syngeography"

The word *autecology* means the branch of biological research in which the responses of the individual *species of animals and plants* are studied in relation to the environmental conditions. On the other hand *synecology* signifies not the species but the *community of organisms, the biocoenosis* (for instance,
36 Krogerus, 1932, p. 190; Thienemann, 1939). However, the non-quantitative determination of the dominant or characteristic species in a particular biotope, or of the more or less regular association of animal and (or) plant species, also falls within the realm of synecology (Bodenheimer, 1938, p. 134). Thus the following section on the "limestone species" is to some extent to be considered as synecology.

In practice, however, the material of synecology can also be used *for quantitative* collection. For this study such collections were not undertaken, so I suppose I should explain why. In my opinion the methods at present favored in zoological synecology (at any rate so far as relates to terrestrial animals) are unsatisfactory. The present situation may be considered under the following heads:

1. A quantitative determination of the carabid fauna of different biotopes or selected sampling areas, without taking into account the other animal or plant inhabitants, would be rather futile. In this way only a small part of the biological group of "consumers" (Thienemann, 1939) would be taken into account. This part cannot be expected to represent a restricted functional unit and consequently a stable large component of the fauna. Even where larger systematic entities, such as the entire fauna of Coleoptera (Brundin, 1934; Renkonen, 1938) are selected as the subjects of quantitative study, from the viewpoint of food biology it means the treatment of only a fraction of the consumer group of the biocoenosis in question. In the case of Coleoptera, besides, it involves a mixture of various types.

On the other hand, anyone who wants to take into consideration the entire (macroscopic) animal world must restrict himself to a very small number of biotopes (for example, Krogerus, 1932; Franz, 1943a).

A quantitative study that takes into consideration only the carabids would actually elucidate nothing more of the "community" of the recorded biotope

than—using a human example—the professional distribution within the family with respect to the business conditions of a city. This is also true of the work of Renkonen (1944), where only carabids and staphylinids are statistically treated. On the other hand, this can naturally be used to take up other questions, especially the problem of competition (cf. p. 554)†.

37 2. Even if we abandon our overall objective to describe the *entire* biocoenosis of a small sampling surface, and thus restrict ourselves to the members of a single group of animals (for instance, insects), to determine their qualitatively and quantitatively changing stock in different biotopes—then too it is essential to give a *detailed description of every sampling area* including its primary inhabitants, the *autotrophic plants*. The persistent dispute as to whether sampling areas should be considered and named according to the nature of their flora or exclusively to the composition of their fauna* is inconsequential here. The most important point is that *the consumers cannot be judged without the producers*, insofar as one actually wishes to causally explain with reasons the existence of one or other species of animals.

However, in synecological investigations the causality is all too often ignored. Most people are satisfied with purely statistical descriptions of the animals or plants of units which are called biocoenoses, etc. and at best make comparisons, mainly quantitative, with other biocoenoses, ignoring the relationships among the members in the biocoenosis under study.

With few exceptions synecology has therefore become a purely *descriptive* science. Its units, the *biocoenoses,* are compared with taxonomic units, the *species* (cf. Taylor, 1935). It is implied that a detailed description possible in the latter, is as important in the former, in order to form the basis for future, more causally-based research. Synecology today should therefore be at the same stage as autecology was at about 100 years ago.

3. But in my opinion it is not appropriate, or even possible, to divide synecological research into a descriptive and a later "causal" period. The synecological unit, the *biocoenosis*, is a far more abstract concept than "the species." It simply represents the mean value of a large series of individuals (of the sampling areas or sampling volumes), and "hybrids" are frequently more common
38 than typical cases. Each of its units possesses a stronger individuality than the individual animals within the species. The relationships between the animal and plant inhabitants of a sampling area must therefore be studied in nature itself and *not only quantitatively.* Even when describing them, the formulation of the problem must be clear, namely: *To what extent are members of the biocoenosis mutually dependent*?

†(cf. footnote page 10; suppl. scient. edit.).

*For literature on the subject see Hesse, 1924, p. 143; Krogerus, 1932, p. 221; Brundin, 1934, p. 42 ff.; Franz, 1939, p. 376 ff.; 1943a, pp. 402, 483; Agrell, 1941, p. 62; Kühnelt, 1943; Tuxen, 1944, p. 171; Backlund, 1943, p. 175; Gisin, 1947.

There is a precondition: *One must be acquainted with the autecology of the organisms.* And that takes us to the main problem: *It is misleading to wish to establish complex units before their components are sufficiently known. Before one is familiar with the autecology of the species, synecology is impossible.* Otherwise we will deal with statistics, using numbers which were achieved in an obscure way, thus are incomprehensible. One can describe H_2SO_4 and utilize it in practice, but its true nature cannot be understood without a knowledge of its components, its basic substances, and their characteristics.

According to Thienemann (1939, 1941), the biocoenosis is "an association of organisms within the same space, in which the individual components of the community have determined, vital relationships with one another." Now these relationships must be determined before one is justified in considering the biocoenosis as a functional unit (see Bodenheimer, 1938, pp. 134 ff.), as an "organism of a higher rank" (Friederichs, 1930, pp. 232 ff.).

4. The prerequisite for expressing the composition of a biocoenosis statistically, i.e. the abundance of its members (of the species or at least the food-biological groups) shows constancy, is that it be "saturated." This indicates that there exists a balance not only among the producers, consumers, and reducers (bacteria and fungi*), as well as the consumers of different levels
39 (herbivore, predator, parasite, etc.), but also "laterally," for instance among various species of predators.

A judgment on this subject hits the most difficult complex of questions in autecology, the problem of *competition* between ecologically related species, which is touched on below (p. 554). It is not possible at this time to decide on the significance of competition. It should be taken only as the expression of a subjective understanding when I assume that the *terrestrial communities of animals are generally not saturated*, at least not constantly.

The basis of such an assertion may be found in the often highly variable number of individuals of a species in different years in the same place, especially among insects. Above all, if the competition factor is strongly influential, one should expect a definite succession of zoocoenoses, especially in newly emerged or much altered biotopes. Here, the stronger competitors among the species that at first have arrived accidentally should gradually become prominent, *even when the vegetation and other environmental factors remain unchanged* (or else after they stabilize). In such a recent region as Fennoscandia, where numerous species of animals are still in the process of spreading out, such a succession of biocoenoses ought to be the rule. To me, however, it appears improbable that it would have remained so completely unnoticed. In the phytocoenoses it is easy to see, for instance on newly formed

*In the soil, fungi are to a large extent nitrogen accumulators. Animals that feed on mycelia (especially acarids; Forsslund, 1943, pp. 167, 175), and thus set nitrogen free may to some extent be considered as reducers. Concerning the significance of other soil animals in the turnover of nutrients, see Franz (1943b).

islands or in burned-over fields.

It may seem bold to oppose on such feeble grounds the assumption apparently shared by most zoosynecologists, as to the "saturation" even of terrestrial animal communities. But it seems to me the onus of proof is on *them*. It would be incomprehensible to simple "farmer's sense" if the animal members of a biocoenosis, with all their fluctuations from year to year and in the course of a single year, were actually capable of using completely all the food afforded by the plants (directly or indirectly) at all times. By far the larger part of the plant material is not utilized as nutrition by animals but is left for the "reducers" (bacteria, fungi, etc.). I doubt there could be any proof that the animals might be able to take over even a certain percentage of these plant materials, so that the normal metabolism of the producers, the green plants, was not deranged. Moreover, part of the nutriment utilized by the animals is passed on to the reducers.

In the limnetic and marine soil zoocoenoses, where the animals are more or less sedentary, the competition factor in my view plays a far bigger part. For that matter water is a far more stable medium than air, so far as temperature, light, movement, etc. are concerned. The abiotic environmental factors, especially the climate, but also enemies and diseases (which represent something different than "competitors"), may exercise an appreciably stronger influence on the constantly changing terrestrial zoocoenoses than the competition factor (see Bodenheimer, 1938, p. 135, and the example given by Elton, 1930, p. 17 ff.). Their influence on various members of the "community" is again a task of autecology.

An extreme example is provided by the three more or less constantly occurring species of animals (two diptera, one snail) of the hot springs ("the absolutely hot springs") of Iceland (Tuxen, 1944). All of them are phytophagous, but competition among them for food could not be established. It is very improbable, since the Cyanophyceae on which they live occur in great numbers. The sole factor responsible for the occurrence of these three species in the hot springs appears to be their resistance to high temperatures, the accurate determination of which is the task of autecology. It is therefore difficult to have understanding what advantages or which higher forms of truth are revealed by considering the species in question as a "community," which is so much emphasized by Tuxen (pp. 59 ff., 100 ff.).

To some extent the above observations are also applicable to plant sociology, which can otherwise function (almost) independently of animal sociology. My reservation refers to the stronger, and at least easier detectable *competition* among individuals and species within the plant community. It is distinctly a competition "for space" (for example, P. Palmgren, 1930, pp. 15–16; Krogerus, 1932, p. 10). In the case of certain trees, such as spruce (*Picea abies*) against pine (*Pinus montana*), this competition is a common knowledge. There is no doubt that the "biocoenotic" factor has a far bigger role in the phytocoenosis

41 than in zoocoenosis. For this reason, statistical data on the number of individuals (density) or the "degree of plant cover" ("Deckungsgrad") within a sampling area may reflect more of a regular reality.

From another viewpoint plant sociology is even worse off than animal sociology, owing to the sampling area-method. A botanist surveys the object he wishes to analyze fairly completely, i.e. the vegetation, even before he demarcates his sampling areas. His choice is not random: it is determined by his conception of what is "typical." The botanist might consider this an advantage, but it really means that with the best of intentions he cannot undertake a study of his object without preconceived ideas. He chooses his sampling areas, and the result of his study, the description of the phytocoenosis, is more or less tainted by his preconceived opinions about its composition. The animal sociologist, who works with terrestrial soil communities, is far more fortunate. In choosing his sampling area he takes into consideration the general (biotic and abiotic) characteristics, including the plant cover, and cannot be misled into a preconceived selection based on the characteristics of the actual object of his study, the faunal composition. The animal sociologist does not need to be that strong in morality!

Like animal sociology, plant sociology is predominantly a descriptive science, which is pursued statistically. In particular, it has an extensive terminology of its own, which often gives the impression of being an end in itself. To what an appalling extent nature is forced into a straitjacket becomes clear from the comprehensive account by Du Rietz (1932) (cf. P. Palmgren, 1930, p. 10).

Naturally, in plant sociology the question of the causes determining phytocoenosis obliges us to indicate the characteristics of the individual species of plant (especially of the dominant species) (for instance, Du Rietz, loc. cit., p. 474). Why then is it not clearly stated that: The *synecology* is incomprehensible without sufficient knowledge of the *autecology* of every plant? Probably because the latter cannot be determined satisfactorily *without experiments*. At any rate the Uppsala school, which is mainly engaged in plant sociological research, is not just indifferent, it is almost hostile toward experimental work. They seem to posit a sixth sense, enabling the trained researchers in the field to pinpoint the area-limiting factor in each case. Actually the most difficult
42 problem, decisive for an understanding of the biocoenosis, is the *factor of competition*, which can be successfully grasped only by experiments. An instance is the "*Taraxacum*" cultures by Sukatschew (1928).

Tansley (1946, p. 27) states: "The 'ideal' method of study might be to investigate each species separately, till we know in detail its life history, the methods by which and the rate at which it could spread, its behavior under different conditions of climate and soil; and only when we had obtained this knowledge proceed to study the species as it existed in communities with other

species."[†] As a plant sociologist Tansley afterwards understandably considers this method as "quite impracticable", with "such complete knowledge" being unattainable. The method is not necessary indeed!

Actually in certain cases exact knowledge of a *single characteristic* (such as the temperature requirement, limestone requirement, parasitism, etc.) of the organism concerned can suffice to explain its choice of biotope. This information is then more important than which biocoenoses the species is a member of. Furthermore, if the method indicated as "ideal" by Tansley is out of reach, it shares this characteristic with all other "ideals", since this very concept implies unattainability. But this does not mean we should not aim toward it.

Finally, comprehensive studies on the *modes of dispersal* of plants are urgently needed. It is a great pity that among the many projects suggested by Sernander just this one is hardly pursued any more in Sweden. If today one wishes to get information on the methods of dispersal of a very common plant of our own flora one still often depends entirely on foreign literature.

At the beginning of the period of plant sociology in Swedish botany the "for" and "against" were expressed in the following significant phrase by Kylin (1923, p. 233) (translated from Swedish): "The different species organize themselves *independent* of one another, according to the ecological conditions." Th. Fries (1926, p. 5) finds this formulation agreeable, but wishes to make a small correction: He wants "independent of" to be replaced by *dependent on*!

43 In my view, the truth lies somewhere between these two concepts. It is senseless to deny the influence of biotic factors among various organisms, but they are not so dominant or so regularly defined as to represent the biocoenoses systematic entities comparable with species, genera, etc. The definition of biocoenosis by Thienemann, quoted above, according to which "the individual components of the community show definite interrelationships which are essential for life," might represent a beautiful thought from Plato's world of ideas.

I prefer the view stated by Uvarov (1931, p. 161): ". . . the theory of stable equilibrium is based on the assumption that the numbers of an organism depend mainly on the numbers of their enemies and on the quantity of food, i.e. on factors which in their turn are dependent on other organisms. No one will deny the controlling value of these factors, but the evidence . . . should go far towards proving that the key to the problem of balance in nature is to be looked for in the influence of climatic factors on living organisms."[*]

Species with more or less similar ecology can be combined in groups (as, for instance, by Larsson, 1939, pp. 433 ff., in the case of Danish carabids). The zoogeographers may also find it appropriate to treat species in groups on the

[†](Original quotation in English; suppl. scient. edit.).
[*](Original quotation in English; suppl. gen. edit.).

basis of more or less similar total or partial distribution. This is *syngeography* in its most modest form.

This branch of study reaches its full development when we pass from groups of species to *surfaces*. Hence the zoogeographical and phytogeographical *regions* are the true counterparts of the biocoenoses of ecology and like them, can be quantitatively (statistically) treated.

The most recent and the best division of Scandinavia into zoogeographical regions and subregions is that by Ekman (1922, pp. 547 ff., Fig. 142; Fig. 2 in the present work). It is predominantly based on the vertebrate fauna.

The carabids are a group so rich in species, comprising so many zoogeographical elements, that they could well form the basis for an independent regional division of Scandinavia or, better, the whole of Fennoscandia. Certain changes in Ekman's map would then be called for. First, the Norwegian "western country" would have to be elevated to the rank of a separate region:
45 its carabid fauna and the beetle fauna in general, possesses quite sufficient *positive* indications (as also the terrestrial mollusk fauna, according to Økland, 1925, p. 149). But the division of the "high boreal region" adopted by Ekman can scarcely be upheld. In particular the "northern Baltic coast" would be too weakly characterized. The birch-tree region (but *not* the more extensive subarctic region in Ekman's sense) ought to be downgraded to a subregion. Within the "south Scandinavian region" doubts arise only in the case of the Norwegian southeastern coast. Otherwise the entomology only confirms Ekman's subregions.

If Ekman's map is compared with one of the more recent phytogeographical maps of the same region (for example, Du Rietz, 1925, 1935; Hård, 1939), irrespective of the changes suggested above, the common features are striking. In particular, the southern boundary of the "high boreal region" and that of the "north Swedish coniferous forest region" are almost identical. Considering Coleoptera, it could be clearly identified in Värmland (the valley of the Klarälv River) (Palm and Lindroth, 1936, p. 40). There are considerable differences only in southern Sweden, where the botanists divide the south Swedish mountain region with a more or less strict North-South line into a "Subatlantic" and a "Central Baltic" region (Hård, 1924, p. 226). This is based for instance on the common occurrence of *Erica tetralix* or the distribution of *Narthecium ossifragum,* but these regions are not sufficiently corroborated by the fauna (see map, Fig. 61).

On the whole, however, the correspondence between the phytogeographical and zoogeographical regions in Scandinavia is so great that the question arises: Is it really necessary or appropriate to undertake separate division according to the zoological and botanical specimens? Would it not be possible to have a synthesis or could one branch of research not utilize the regions recognized by another? These questions recall the corresponding and likewise different views concerning the foundation of biocoenoses.

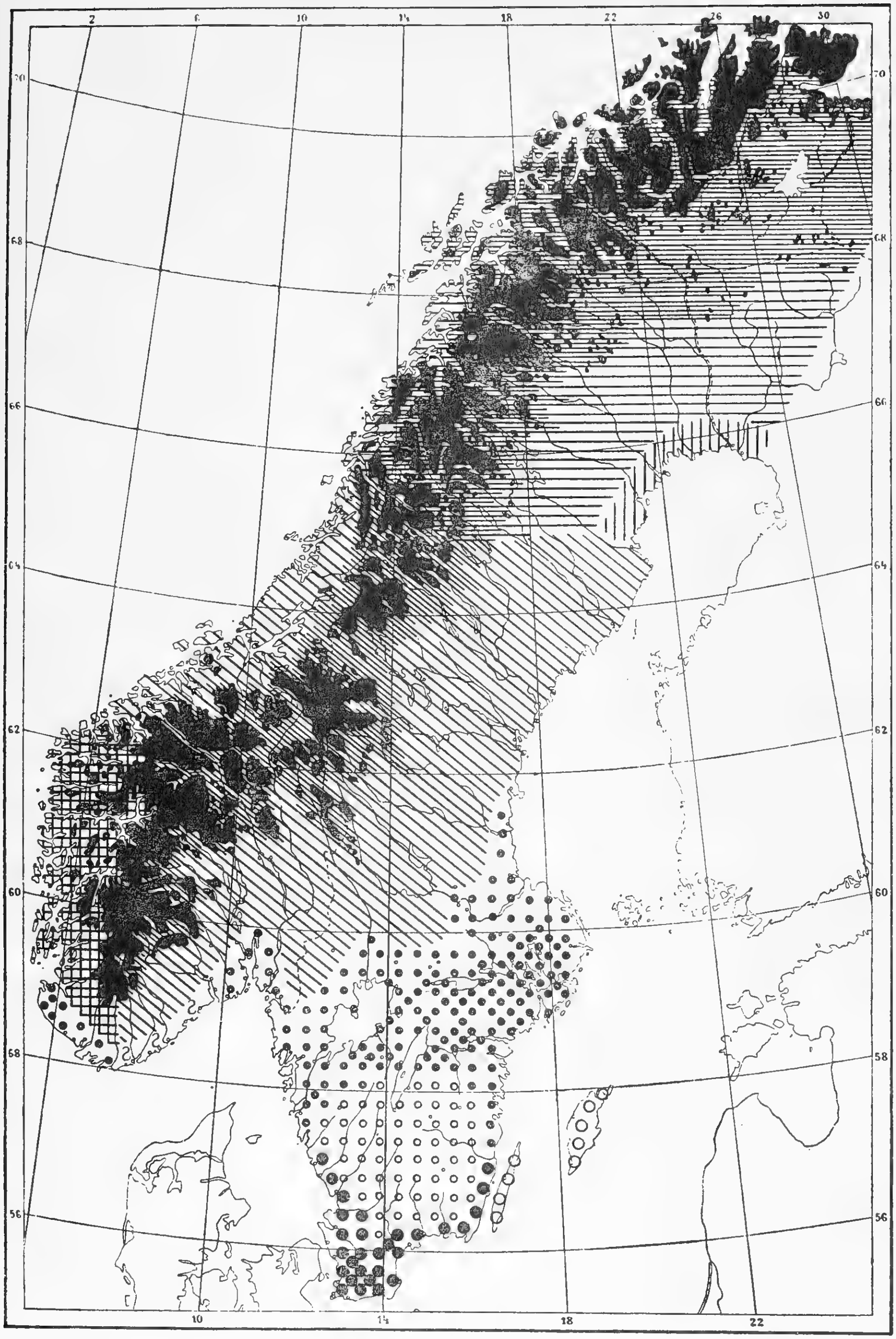


 Fig. 2. The zoogeographical division of Scandinavia. (After Ekman, 1922, p. 576).

"The regional zoogeography should divide the earth into regions that express the actual distribution of animals and the phylogenetic correlation of the faunas as truly as possible" (Ekman, 1940, p. 18). On the other hand, Reinig (1937) exclusively follows the historical method, which is believed to "reveal the centers of evolution," "centers whose characteristic is more lasting and more easily comprehensible than the very hypothetical boundary lines of
46 organized zoogeography" (l.c., p. 72). By "centers of evolution" Reinig understands glacial refuges.

Study of the glacial history offers by far the most important basis for judging the present-day fauna of the Northern Hemisphere. However, one fully agrees with Ekman when he rejects this viewpoint as the sole guiding principle, since it has to be pursued with altogether too many purely hypothetical preconditions.

Regional zoogeography is therefore primarily a descriptive science, and one might expect that on account of its relative objectivity it would lead to fairly unequivocal conclusions. Quite the contrary. Let us compare the two maps of regions by Holdhaus (1929) and Semenov (1935), based on entomogeographic facts. The former covers the entire globe and the latter the Palearctic Region. Even apart from the fact that Semenov's map divides the subregions into provinces there are considerable differences, especially in Central and Eastern Asia. If other animal groups are considered, still greater divergences result. It is scarcely an exaggeration to state that every zoogeographer dealing with these questions in detail has his own system. An example of setting up a very unnecessary faunistic province is "the northern temperate, east Atlantic faunal region" (Iceland, The Faeroes, The British Isles, ? northwestern France, ? western Norway) named by Braendegaard (1932, p. 33).

What then is the purpose of these regions, including all of their subdivisions? Is it arrangement ("Ordnung") just for the sake of arrangement? The regional boundaries are often so ill-defined and the results so diverse, depending on the group of animals considered, that one is inclined to take this irreverent view. And any future incorporation of the *entire* terrestrial fauna into *one* regional system would certainly be so full of compromises that the transitional zones would occupy a larger total surface than the regions and their subdivisions.

Where the regional zoogeographical boundaries are sharp, for example, the northern boundary of the Mediterranean Region and the forest-steppe boundary in Asia, they coincide almost without exception with the *phytogeographical* boundaries. The two most distinct zoogeographical boundaries in Scandinavia are the timber line in the fjelds[†] and the southern boundary of the northern coniferous forest region. So I do not consider it a misfortune not to have a special zoogeographical division of Fennoscandia into regions.

[†](= barren plateau of the Scandinavian upland; suppl. scient. edit.).

47 Regional zoogeography can under no circumstances be studied without plants, especially the forest patterns, and, besides, these are the most concrete exponents of the climate of the landscape.

My answer to these questions is: *At least within limited geographical regions it may be practicable for the zoogeographer to accept the phytogeographical regions and work with them as units.* For my purpose the map of the forest regions of Fennoscandia (Fig. 61) sufficed. I was chiefly concerned with an evaluation of the climatic requirements of the individual species according to their distribution in different "regions," including the high altitude belts of the fjelds.

The most important task of regional zoogeography is not delineation and description of regions along with divisions of a lower rank but comparison between the faunal stocks of the larger or smaller regions. This should stimulate causal research, especially a historical reflection. I do not know whether such faunal stocks have a homogeneity comparable with the large phytogeographical regions of the earth, but I think they may well have.

It need not be especially emphasized that the above discussion relates only to the regional geography of *terrestrial* fauna. The marine, and to a greater or lesser extent the limnetic fauna is not directly dependent on the plant world.

The content of this section has a distinctly negative character, and betrays the author's limited understanding of every form of collective treatment of the species of animals and plants. This is due to his humble acknowledgment of *the species* as, in any case, a relative physiological entity, whose responses must be studied, before it can be combined with other entities into larger categories. This is because "every grouping of the material all too easily conceals the basic fact *that every species poses its own problem.*"

Analytic Part

48† **The Realized Experiments**

The experiments represent an attempt to isolate the external factors which operate on the animals in nature and to judge their influence. However, isolation signifies something unnatural. For instance, we can never claim to know the accurate temperature preferendum of any particular species, because there is no such thing. It is among other things dependent on humidity. It would of course be possible to determine the temperature preferendum for a particular stage of the animal at constant humidity of the air, but this too would not determine any "natural" complex of factors. In nature it is namely the most essential point how the animal in its biotope reacts to daily and yearly changes, amongst other things to exactly those of temperature and humidity. And these facts can be determined only on the spot, by means of extensive microclimatic measurements, which are not available at present. —Besides, the same species may respond differently at different times (even in the adult stage), many examples of which are given below.

These and other considerations directed me towards always obtaining the *comparative* values in all experiments. This means that every experiment was *carried out,* if possible, simultaneously (or at least under similar external conditions, as far as possible) with *two or more species* which, if possible, were collected at the same time and kept in captivity under identical conditions. It is best to select two systematically closely related species, differing in their distribution or ecology. If the experiments show a correspondingly different response of these species one may then be justified in seeking the cause of their different behavior in nature within the established complex of factors.
49 So too when unrelated species that are more or less identical in the aspects mentioned show *similar* responses in the experiments. —Nevertheless, we are still far from this and from any determination of the exact decisive factor, which indeed is unattainable so far as my experience goes.

A further reason for my relatively modest expectations from these experiments is that they were conducted under primitive conditions with simple

†(Pagination of the original German version, to which page citations in the text of this translation are referring to; suppl. scient. edit.).

instruments in the open air, in my apartment house, or in the laboratory at my school (only the experiments using a refrigerator were carried out in Statens Växtskyddsanstalt, Stockholm). For instance, the possibility of controlling the humidity of the air in the experimental room was extremely limited. Under such conditions it would be wrong to expect "accurate values."

The weakest point of all my experiments is undoubtedly the fact that only the responses of *adults* were studied. Only in two cases was adequate larval material available. In one case, *Pterostichus anthracinus,* the larvae were reared for genetic studies (Lindroth, 1946), and I did not venture to jeopardize them by other experiments. In the other case, *Oodes gracilis* (Lindroth, 1943a), the "response points" were actually determined (l.c., Diagram 6) and a temperature gradient apparatus ("*Temperaturorgel*") experiment was also run (l.c., p. 136). This did not succeed because the larvae in the cold part of the apparatus immediately became torpid.

The greatest differences between the larva and the imago are not to be expected in the preferenda values, since the parents, at least during the breeding period, must of course seek the most suitable biotopes for their young ones, i.e. at least at this time they possess the same or very similar preferenda. But the resistance values, for instance the range of the activity temperature largely determined by the "lower response point" (see p. 104) would no doubt usually show greater sensitivity for the larva, which was revealed by experiments with the larvae of *Oodes gracilis* (see above). The species used in such experiments, with few exceptions (*Amara equestris, Calathus* and *Cymindis*), were *imago hibernators.* They experience the critical periods, i.e. spring and autumn (at any rate with regard to temperature) in the adult stage, and the responses of the adults may therefore actually be decisive.

As far as the humidity of the air and soil is concerned, the summer is probably more fateful and hence also affects the larvae. The results of the experiments with such factors must therefore be treated with greatest caution.

50 It may be justly objected that my experiments were all conducted with too little material. But one must consider the many very diverse questions asked by these experiments and therefore greater concentration, otherwise very useful, became impossible. Superficiality was the price for tackling so large a task. Also, some of the species used are so uncommon that more material could not be efficiently gathered.

Finally, it should be mentioned that it is best to use about equal numbers of males and females in experiments. In many cases (which it is unnecessary to justify at this point) I kept the sexes separate and found no constant differences. But it is conceivable that there could be differences.

The most important sources of error intrinsic to different designs of experiment are assessed below with the description of each apparatus. Here only some series of experiments will be described, those of prime significance for any judgment of all other aspects.

1. A fundamental question is *whether the different behavior of the individuals of a species of animals in the experiments* (especially the preferenda experiments) is *due to individually different* (hereditary or environmentally determined) *characteristics or is only fortuitous.* It would be especially important to decide whether that difference is between markedly *stenotopic* (especially stenothermic) and distinctly *eurytopic* (especially eurythermic) species, which is manifested in the experiments by a greater dispersion of the eurytopic species in the apparatus (particularly in the temperature gradient apparatus). Is this difference to be understood as meaning that a eurytopic species is more heterogeneous, i.e. consists of a larger number of physiologically different "biotypes," or that in each individual there is a different sensitivity toward the factor studied?

Pterostichus nigrita turned out to be a suitable experimental animal. Compared with *P. anthracinus,* it shows not only a lower temperature preferendum (12.4°C as against 20.2°C; Experiments 27, 26a, p. 72) but also a considerably greater dispersion in the gradient apparatus (Diagram 1). As a geographically and ecologically ubiquist, the species also shows a pronounced eurytopy.

51 Each of the 15 specimens of *P. nigrita* was differently marked with zinc white and their sequence (but not the exact temperature preferendum of every animal) in the temperature gradient apparatus was noted in 10 successive experiments. The result (Diagram 2) shows that the relative placement of every individual was as good as random. The "coldest" animal (d), in all 10 experiments, of course stayed in the colder half, but settled down at the lowest temperature only three times. The "warmest" animal (l) on six occasions remained at the highest temperature, but once even entered the colder half. The medium preferendum as well as the dispersion* figure (mean deviation of all insects from the medium preferendum) would not significantly change even if both these "extreme" animals were excluded†. The following statement therefore seems justified: *The eurythermic character of Pterostichus nigrita is not (or is only slightly) due to physiological heterogeneity of the populations, but to the insensitivity of the individuals.* Although further experiments with other species would be desirable I am inclined to assume that the same principle holds well for all *eurythermic* (and generally eurytopic) species. It does not follow that such species do not form physiological races, or that populations in distant parts of the total area of a widely distributed species would necessarily be physiologically alike. But the eurythermic character of a species
53 that is geographically and ecologically ubiquitous must be primarily due to its less specific requirements for life. Conversely the stenotopic species have sharply specific requirements. Or they are stenotopic only at the periphery of

*I was prevented from investigating the two "extreme" specimens of *Pterostichus nigrita* more closely in comparative temperature experiments because one of the insects perished.

†(Contradictory to the ecological term "dispersal". cf. p. 203; suppl. scient. edit.)

their area, close to the minimum of a particular factor, and may then occur elsewhere as more or less eurytopic species.

The following case may be cited as an example of individual behavior in the temperature gradient apparatus (Experiment No. 17b, p. 72); 17 specimens of *Harpalus punctatulus* were tested after 4 months in captivity. Five specimens were collected positively at the cold end (about 12.5°C), where they became torpid, whereas the remaining individuals did not settle down at temperatures below 17.8°C. The five "cold" individuals which were thereafter subjected to a new temperature gradient apparatus experiment (Experiment 23b, p. 72), again stayed (despite the use of H_2SO_4 at the cold end) at the lower temperatures (11.9 to 15.6°C) than the other 12 specimens. —Individually different response in the temperature gradient apparatus in the case of *Calathus erratus* and *Harpalus pubescens* has also been observed by Agrell (1947).

It is usually impossible to decide whether such individual differences in response are due to a fortuitous physiological condition (for instance, the age of the insect) or whether they are genetically determined.

2. The second major question therefore concerns the *constancy of the responses of a particular species of animal.* How much do the responses of the individual observed during the experiment depend on environmental factors and how much on the internal physiological condition (such as age)?

I have already touched on this question (Lindroth, 1943a, pp. 136–137) with regard to *Oodes gracilis* and *O. helopioides.* In the temperature gradient apparatus (Diagram 3), the former showed a *stable* preferendum, which always stayed at +20°C, irrespective of the environmental factors, whereas *O. helopioides* exhibited a *variable* preferendum. This "unmistakably varied according to the initial temperature on the day of the experiment" (or eventually increased during the summer, independent of small variations in the day temperature). Similar results were obtained by Herter (1923, p. 284) in experiments with *Formica rufa* L., and by Bodenheimer and Schenkin (1928,

51 Diagram 1. Distribution of insects in the temperature gradient apparatus ("Temperaturorgel"). A—*Pterostichus anthracinus* (Experiment 26a, p. 72; 17 specimens); B—*P. nigrita* (Experiment 27, p. 72; 19 specimens).

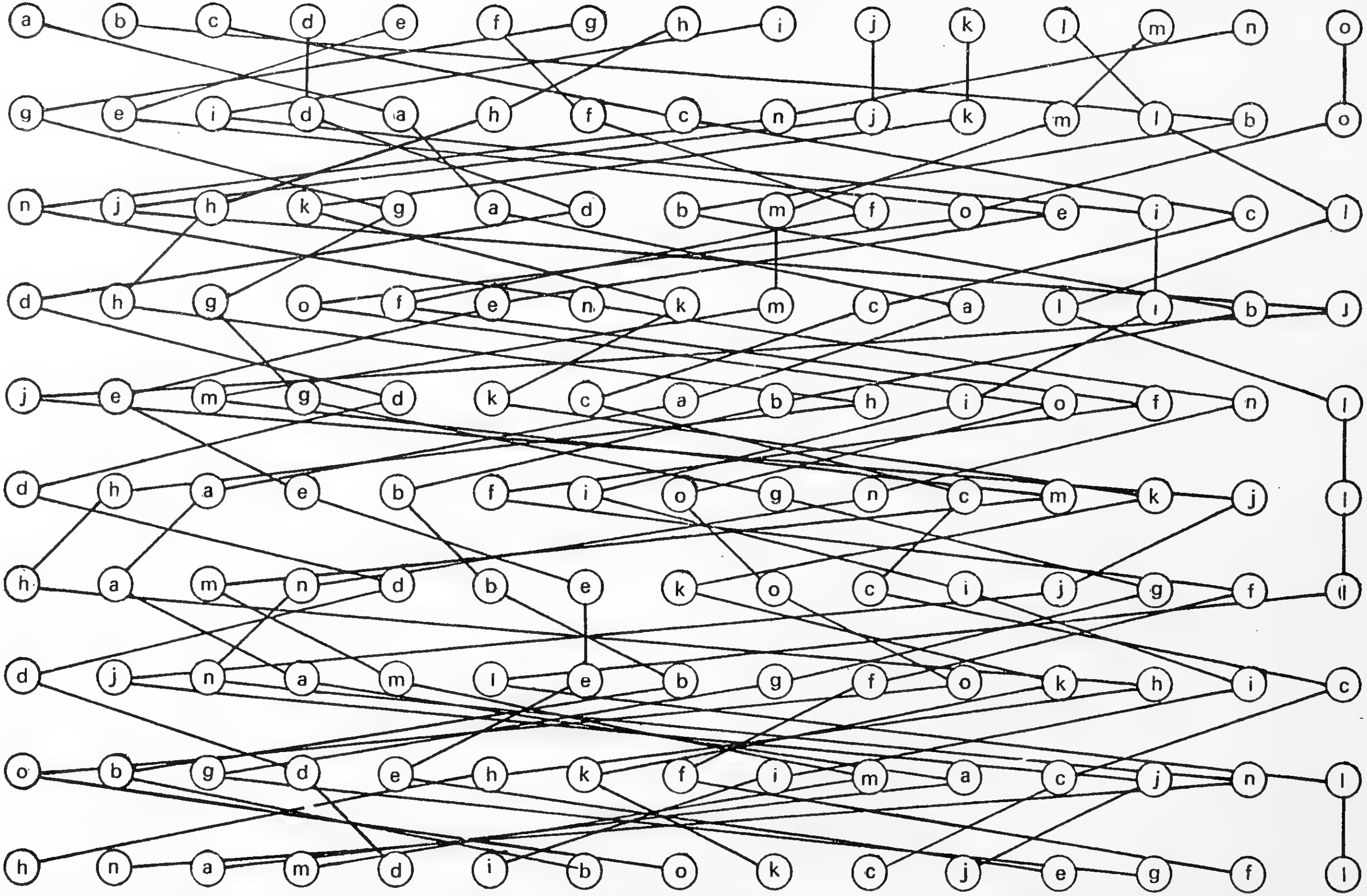
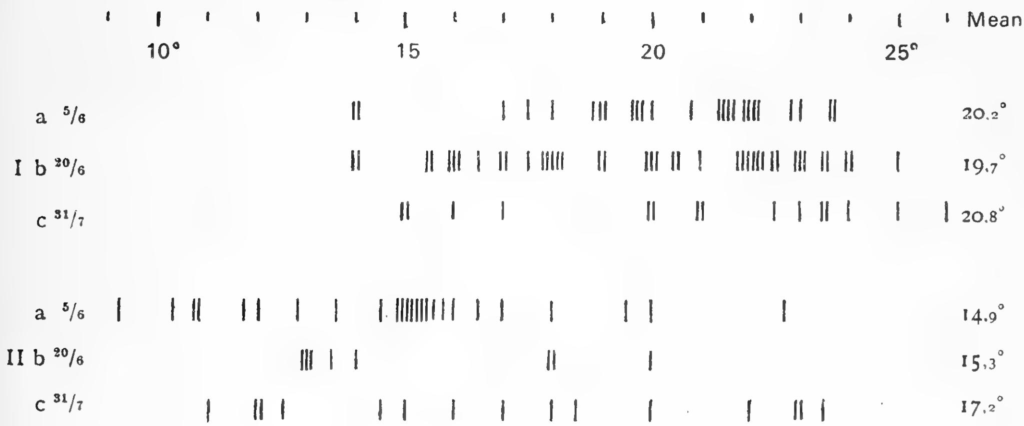


Diagram 2. *Pterostichus nigrita*. Temperature gradient apparatus. Sequence of 15 marked specimens (a–o) in each of 10 successive experiments (Experiment 28, p. 72). Cold end of gradient apparatus is on left, warm end on right.

pp. 3, 10) with storage pests. In *Calathus erratus* and *Harpalus pubescens,* Agrell (1947) found a distinct decline in the preferendum after four days' exposure of the test animals to a low temperature (+10°C). He got the same result af-
54 ter exposure to a higher temperature (+30°C). In nature the latter response, with the exception of markedly cold-seeking species, has an insignificant role, since high enough temperatures rarely occur and usually can be avoided by the animals through active movements. A prolonged period of thirst (Heerdt, 1946, p. 28) or hunger (Agrell, 1947) also causes a decline in the preferendum.

The specimens of *Oodes* available for observations was very low in number. However, experiments with other species have shown that this division of species into those with a "stable" and those with a more or less "variable" temperature preferendum (which evidently show no sharply distinct types) is justified.

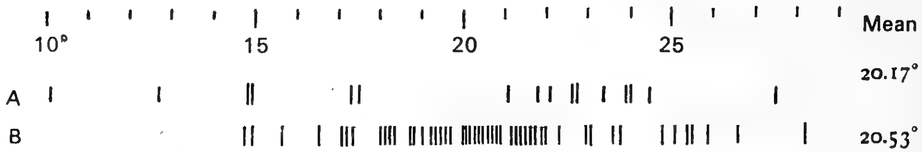
Pterostichus anthracinus provided highly suitable test material, of which both, freshly collected animals (Upl Djursholm) and animals of the next generation, bred from these in the laboratory, were tested in the temperature gradient apparatus. All animals therefore belonged to the same population, but the parents, which had hibernated as adults, had been subjected to all the changes of weather in nature. However, the animals of the following generation had passed their lives at constant room temperature (about 20°C) from the egg on (May through August). The temperature gradient apparatus experiments
55 (Diagram 4) showed a medium preferendum on the part of the parents of 20.2°C, and on the part of the new generation of 20.5°C. The dispersion of field animals was of course somewhat greater. The insignificant difference is



54 Diagram 3. *Oodes gracilis* (I) and *O. helopioides* (II). Distribution in the temperature gradient apparatus on three different dates (a, b, c). After Lindroth, 1943a.

within the limits of experimental error or chance, all the more as the parents numbered only 17 specimens. It can therefore be stated that *Pterostichus anthracinus* is distinguished *by an unusually stable temperature preferendum.* The highly variable environmental factors have exercised no demonstrable influence in this case, nor the fact that in one case hibernated individuals more than one-half year old were taken and in the other less than two-month-old adults.

Harpalus serripes (Diagram 5) also shows a remarkably stable temperature preferendum. Freshly collected insects showed (during early May, 1945) a median preferendum of 27.89°C in the temperature gradient apparatus and a dispersion (mean deviation) of only 1.95°. During late August, after four months of captivity indoors, the values obtained from the same animals were almost
56 exactly the same: 27.93°C and 2.13°C. Only in the following year, by which time the 12 survivors of the original 23 individuals in every respect looked weak and infirm with age*, did their responses decline. The medium preferendum then was 25.9°C and, significantly, the dispersion had increased to 4.8°.



55 Diagram 4. *Pterostichus anthracinus.* Temperature gradient apparatus. A—Field specimens (P generation); B—F_1 generation bred from them. Experiment 26 a, b–c, p. 72.

55 Diagram 5. *Harpalus serripes.* Temperature gradient apparatus. A—Freshly collected field material; B—After 4 months in captivity; C—After 14 months in captivity. Experiment 23, p. 72.

*However, the last specimen of *H. serripes* lived until January, 1948 thus became more than three years old.

Brachynus crepitans (Diagram 9; see also p. 60) behaved similarly, with its medium temperature preferendum of 25.87°C after $4\frac{3}{4}$ months in captivity. In the case of freshly collected material the value was only slightly higher at 26.65°C. The dispersion in the former case was likewise only slightly greater, 3.2° as against 2.5°.

Low stability was shown by *Harpalus punctatulus* (Diagram 6), which was collected simultaneously with *H. serripes* and was similarly treated. During spring the medium temperature preferendum was 27.08°C, with a dispersion of only 1.65°. After four months of captivity, however, it was 21.06°C and the dispersion had risen to 4.74°. It is probably not primarily the decrease of the temperature preferendum but the increased moisture requirement (possibly due to abnormal conditions in captivity; cf. below), which automatically must cause this effect. In nature a corresponding variation with the temperature is not demonstrable in this species. On June 25, freshly collected specimens showed a medium preferendum of 28.83°C and a dispersion of 1.53°.

Normally the lability† of the preferendum, when significant, might be considered as a physiological adaptation to the environmental temperature, which is expressed by increasing values during summer. In addition to *Oodes*
57 *helopioides* and *Harpalus punctatulus,* which were studied, *Harpalus melleti* and *H. rupicola* appear to behave similarly. At the beginning of May the species showed (Diagram 7) a medium preferendum respectively of 23.04° and 18.07°C (dispersion of 3.07° and 2.06°, respectively). But in late June (fresh material) it was respectively 26.98° and 23.81°C (dispersion 1.47° and 2.33°, respectively).

Especially in eurytopic and widely distributed species a labile temperature preferendum might be normal. The question calls for a thorough investigation based on more extensive material, and the explanation should be sought in purely physiological terms. From the results so far obtained it appears at any rate that populations that respond differently in the experiments must not

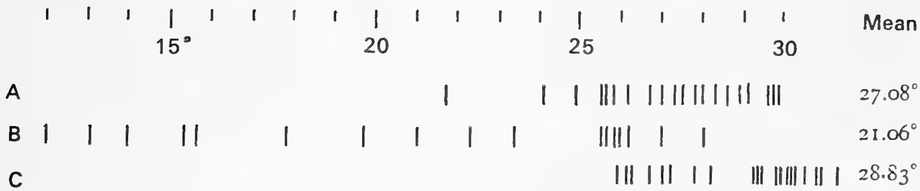


Diagram 6. *Harpalus punctatulus*. Temperature gradient apparatus. A—Freshly collected field material (early May); B—After 4 months in captivity; C—Freshly collected field material (last June). Experiment 17, p. 71.

†(= ecological term: suppl. scient. edit.).

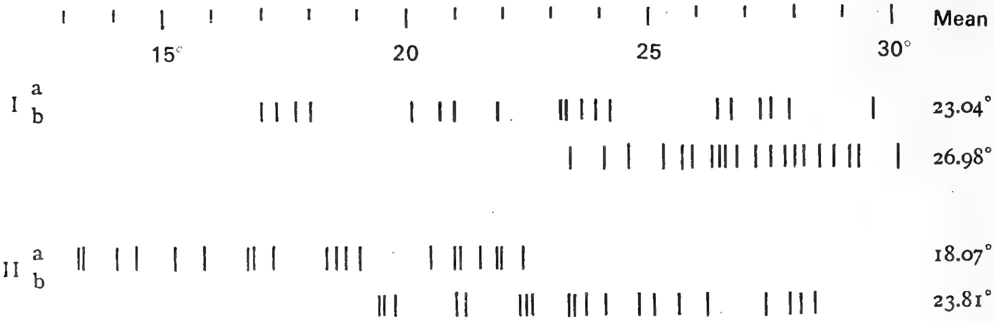
be just declared as constitutionally different, because if we are dealing with "labile" species they may be in different stages of adaptation.

It might also be possible to determine this adaptability of some animals with other preferenda experiments (but apparently to a lesser extent with resistance experiments). The behavior of *Harpalus punctatulus* in the "humidity gradient apparatus" ("Feuchtorgel") might be cited here as an example (Diagram 8).

Twenty-one specimens were collected in late April, 1945. After three weeks in captivity they were tested in the "humidity gradient apparatus" (Experiment 72a, p. 79). The attraction toward the dry end of the humidity gradient apparatus was as strong as in *H. serripes* (Diagram 22, p. 134). The
58 following year, freshly collected material (75 specimens) were tested in the same way in late June (Experiment 72b). The animals distributed themselves fairly uniformly in the apparatus, whereas *H. serripes* (150 specimens) always showed (Diagram 21) a clear attraction to the dry boxes. If the boxes are numbered 1 to 7 from the dry to the moist part of the apparatus we can calculate the "mean box" in each test. This rose from 2.8 to 4.2 in *H. punctatulus* but from 2.8 to 3.4 in *H. serripes.*

The corresponding experiments in the "universal gradient apparatus" ("Universalorgel") (Experiment 112b; Diagram 29) were even more clear. The mean box place (10 boxes) increased in the same specimens, which was tested in June (after 2 months' captivity) and in August (after $3\frac{1}{2}$ months), in *H. punctatulus* from 3.65 to 6.5, but in *H. serripes* (Experiment 116b, Diagram 33) from 3.85 to 4.3.

59 Assuming that environmental factors (conditions in the culture container) could have influenced *E. punctatulus*, because the animals were, for instance,



57 Diagram 7. *Harpalus melleti* (I) and *H. rupicola* (II). Temperature gradient apparatus, using freshly collected field material. a—Early May; b—Late June. Experiments 15, 21, p. 71.

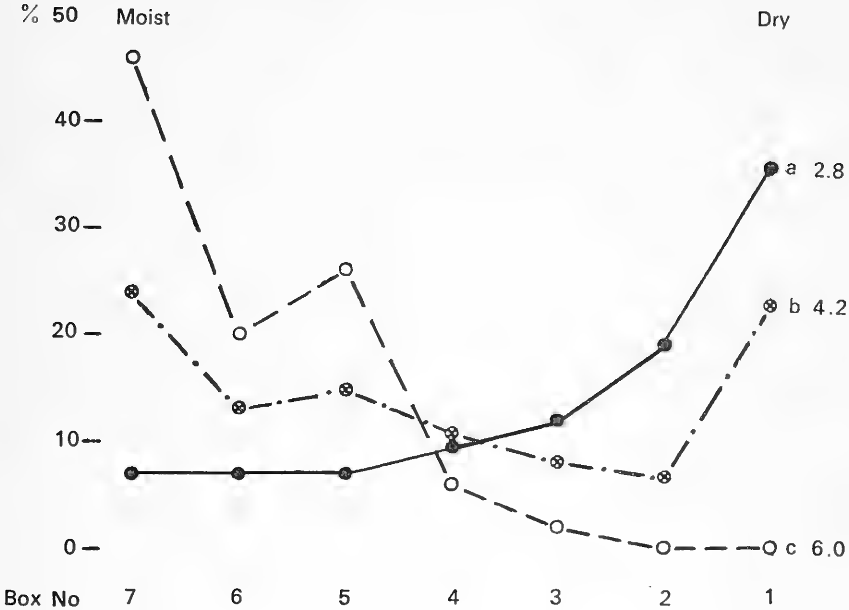


Diagram 8. *Harpalus punctatulus*. Distribution according to varying humidity in the substratum gradient apparatus ("Substratorgel"). a—May, after three weeks in captivity; b—June, after one week in captivity; c—July, after two weeks in captivity and two days' confinement in moisture-saturated air. "Mean box" is noted on right. Experiment 72, p. 79, Diagram 16.

kept too dry and were thirsty, I kept them (50 specimens) for two days with moisture-saturated air and again tested them in the humidity gradient apparatus (Experiment 72c). The result was surprising. The distribution was exactly the reverse from that obtained in spring, i.e. a strong clustering in the *moist* end. Evidently the water balance of the animals had greatly altered during their stay in damp air.

The lability of the moisture preferendum of *Harpalus punctatulus* is evident from these experiments. It can be altered by a change in the environmental factors and besides, an increase in the humidity requirement evidently takes place during summer. Thereby (as shown on p. 56 and on p. 67) the temperature preferendum is also affected (lowered), but conversely the environmental temperature has certainly a considerable influence on the water balance of the animal. Specific studies should be able to reveal which factor is primary. On the other hand, according to Bodenheimer (1931, p. 741), in *Calathus fuscipes* the temperature preferendum is independent of changes in the humidity of the air.

From the practical experimental viewpoint the above examples show that

in some species *absolute* response values cannot be achieved, and that the species to be compared must, so far as possible, be represented by equal material (of the same age, similarly treated, studied at the same time of year, etc.).

3. In nature many factors simultaneously influence individual animals and the species. It is usually extremely difficult to decide *which of the factors* (throughout the area or in some part of the area) *is the most important.* An attempt to approach the problem more closely by studying the influence of one or more factors experimentally at the same time is represented by the "universal gradient apparatus" described below.

But a special case may be discussed here, whereby the question is approached as it were through the back door, that is the case of *Brachynus crepitans* and *Agonum dorsale.*

These two species are such obligatory companions that *Brachynus* actually never occurs without the *Agonum* species (on the other hand, *Agonum* can live without *Brachynus*, as for instance in Skå). The distribution maps, especially for eastern Sweden, are therefore almost identical. This relationship led to
60 the belief that *Brachynus*, whose development is still unknown, was associated with *Agonum* as a parasite. As mentioned elsewhere (p. 548), this assumption is erroneous. Neither of the two species is associated with the other through food biology.

Brachynus crepitans and Agonum dorsale thus represent a rare instance of two species that show exactly the same ecology and almost the same distribution on account of their identical life requirements. It is therefore natural to test both the species together in all the usual preferenda and resistance experiments, in order to determine the factors to which they respond most similarly. It may then be concluded that *these* factors are the decisive ones.

The following experiments were conducted:

a. *Temperature preferendum* (Diagram 9; Experiments 1 a–d, 6 a–e).

In all concurrent experiments *Brachynus* thus shows a higher temperature
61 preferendum than *Agonum dorsale.* Because of this the dispersion in the latter species is somewhat less. The mean temperature preferendum for all the experiments is*:

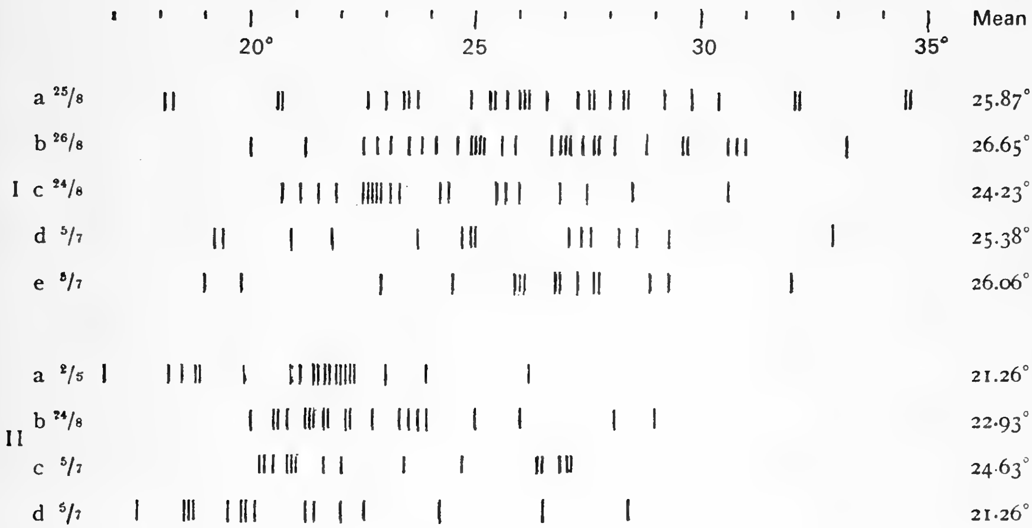
Brachynus (110 specimens) 25.64°C , dispersion 2.67°C.

Agonum dorsale (70 specimens) 22.52°C, dispersion 2.15°C.

b. *The response points of temperature.*

The *lower* limit of activity (Experiments 124, 128, 129), i.e. the temperature at which the animals became motionless after supercooling, was determined concurrently on a total of 42 specimens of each species. The following figures were obtained:

*The total mean values were calculated without taking into consideration the number of individuals used in each experiment.



60 Diagram 9. *Brachynus crepitans* (I) and *Agonum dorsale* (II). Distribution in the temperature gradient apparatus on different dates. Data of each experiment noted on left. cf. Diagram 11, Experiments 6 and 1, pp. 69–70.

Brachynus: 4.1, 4.4, 5.9, 6.4, 6.4, 6.8, 6.9, 7.0, 7.6, 7.6, 7.7, 7.7, 7.7, 7.7, 7.7, 7.8, 7.9, 8.0, 8.1, 8.4, 8.5, 8.5, 8.6, 8.6, 8.7, 8.7, 8.8, 8.8, 8.8, 8.9, 8.9, 8.9, 9.1, 9.5, 9.6, 9.8, 10.5, 10.5, 10.7, 10.8, 11.0, 12.6.

Agonum dorsale: 6.5, 6.6, 6.8, 7.4, 7.5, 7.5, 7.6, 7.7, 7.7, 7.7, 7.8, 7.8, 8.0, 8.0, 8.1, 8.1, 8.1, 8.2, 8.2, 8.3, 8.3, 8.4, 8.6, 8.6, 8.6, 8.7, 8.7, 8.7, 8.7, 8.8, 8.8, 8.9, 8.9, 9.0, 9.1, 9.5, 9.5, 9.6, 9.8, 9.8, 10.0, 12.2.

The mean values, 8.35°C (*Brachynus*) and 8.45°C (*Agonum dorsale*) respectively, are so close that they may be considered identical.

However, the *upper* limit of activity (Experiment 137) was very different. The temperature at which the first sign of paralysis appeared, and that at which total paralysis resulted, were measured individually on 20 specimens each. Since the figures are very close together, enumeration is unnecessary.

	First sign of paralysis	Total paralysis
Brachynus	46.2–49.6°C	48.8–54.2°C
Agonum dorsale	42.4–47.1°C	42.8–48.8°C

The mean values for *Brachynus* are 48.7°C and 51.0°C and for *Agonum dorsale* 45.5°C and 47.1°C. Thus in both cases there is a difference of 3–4°C.

c. *Humidity preferendum* (Diagram 10; Experiments 82, 83, p. 80).

This was determined in the circular universal gradient apparatus, since the usual substratum gradient apparatus is unsuitable for these non-digging insects. In recording three observations every second hour, 120 observations were obtained in each case. The calculated mean box place for *Brachynus* is 3.1, for *Agonum* 3.0, thus showing an extremely close relationship.

d. *Drought resistance* (Experiment 141).

The length of time for which the animals were able to live without water
62 was determined for 20 specimens each of the two species. The mean maximum duration of life in *Brachynus* was found to be 137 hr 45 min, and in *Agonum dorsale* 123 hr 48 min—a difference of more than half a day.

In these fairly closely correlated experiments with *Brachynus crepitans* and *Agonum dorsale,* which have the same ecological requirements in nature, *the two species exhibited such close similarity with regard to temperature for the lower limit of activity and their moisture preferendum that these values may be considered identical.* Hence the conclusion that *among the factors measured* (and among all those measurable?) *these two are decisive for the species concerned.*

Evidently this conclusion must not be applied too freely to other animals. For instance, in the hygrophilous species of *Oodes* the preferenda appear to give a more correct indication of the temperature factors decisive for life than of the "lower response point" (p. 457; also see Lindroth, 1943a, p. 137). However, it seems at least justified to suppose that the factors decisive for *Brachynus* and *Agonum dorsale* can also be especially important for other more

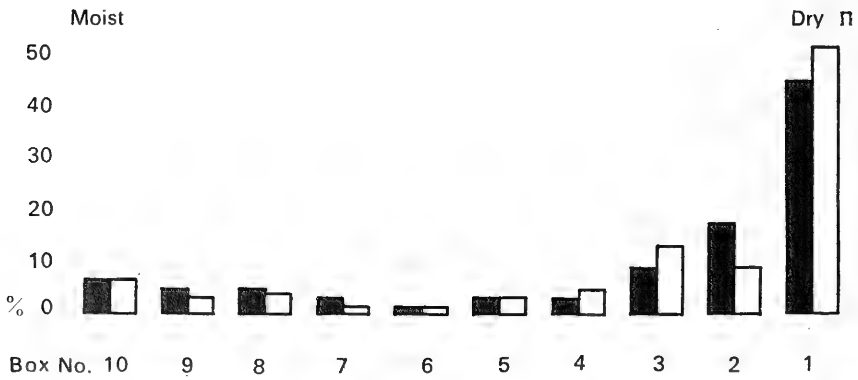


Diagram 10. *Brachynus crepitans* (black) and *Agonum dorsale* (white). Distribution during a common experiment in the "humidity gradient apparatus." Experiments 82, 83, p. 80.

63 or less xerophilous carabids. Accordingly they have been considered important in the treatment of the "limestone species," among others.

Finally, it should be mentioned that I have not analyzed the data obtained from the experiments by the latest method of statistical analysis (as in Bonnier and Tedin, 1940). The mean values have only been calculated arithmetically and, besides, the *dispersion index* has also been given, i.e. the mean deviation of all the experimental animals from the calculated mean value.

As an example how the mean values turn out by one or the other method, I have also analyzed the above temperature gradient experiments with *Brachynus* and *Agonum dorsale* with the statistics of variation (after Herter, 1924, pp. 234–236). The observations were divided into frequency classes of 2°C each (Diagram 11); these calculations are presented in Table 1. The mean values differ only slightly from the arithmetic mean.

Unfortunately I have had absolutely no schooling in mathematics. Nevertheless I would venture to cast doubt on the validity of applying purely mathematical methods to an analysis of the temperature gradient apparatus experiments. The distribution of insects in the gradient apparatus (and hence the values obtained by interpolation) does not appear to me purely accidental. It can be easily observed (as discussed on p. 69) how the animals show a choking effect as soon as they come from their more or less broad zone of preferendum towards the *warm* end of the apparatus, whereupon they hastily turn back. On one side of the *preferendum* zone there is, so to speak, a *barrier*, which has no counterpart on the other side (i.e. towards the cold end). The deviations from the mean value (whether obtained arithmetically or statistically) are therefore *not determined fortuitously*.

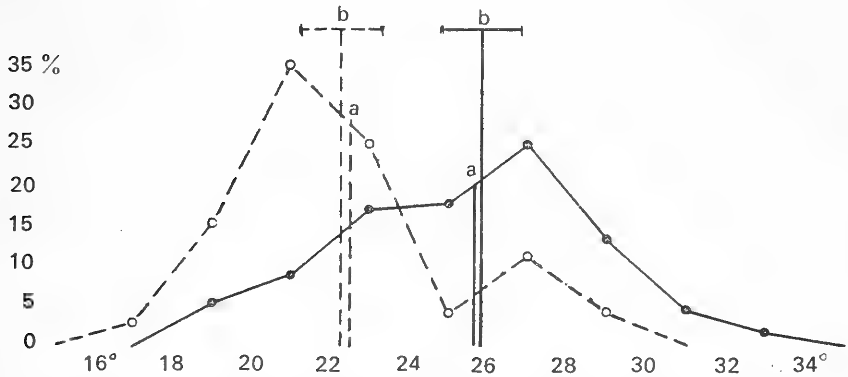


Diagram 11. *Brachynus crepitans* (continuous lines) and *Agonum dorsale* (broken lines). Frequency curves of temperature preferenda according to Diagram 9. a—Arithmetic mean value; b—Statistical mean value, and calculated amplitudes of variations of latter (horizontal lines).

Table 1. Statistically calculated figures obtained from experiments on *Brachynus crepitans* and *Agonum dorsale* (Diagrams 9, 11) with the temperature gradient apparatus

	M +°C	m °C	M ± 3 m +°C	σ °C	n
Brachynus crepitans	25.836	± 0.345	24.802–26.870	± 3.620	110
Agonum dorsale	22.286	± 0.341	21.263–23.309	± 2.854	70

Note: M—Mean value; m—Mean error thereof; σ—Standard deviation; n—Number of observations.

Probably because of this the calculated mean preferenda are consistently too low. But it is more important that different species behave differently toward the "heat barriers." In the case of *some species,* such as *Brachynus,* the response starts after contact with the highest temperature, such that they usually proceed toward the cold end of the apparatus without resting. In the case of *others*, such as *Agonum dorsale*, the same stimulus usually causes only lesser movements. This difference is clearly evident when the curves of the two species are superimposed (Diagram 11). I even believe that the strange growth of the "27° frequency class" of the *Agonum* curve resulted from the aggregation of individuals that were repulsed by the heat barrier.

65 Another manifestation, which is evident especially in most of the experiments with the universal gradient apparatus (Diagram 25 ff., p. 141 ff.), is that the more or less distinct preferendum zone (hence the "main maximum" of the diagram) is demarcated by a distinct minima on one or both sides, after which the curve rises steeply. The probable explanation is that the preferendum zone in the immediate vicinity of the insects exercises especially strong "absorption" on them—further evidence that the animals are not distributed accidentally outside their maximum of frequency.

Also the striking association of various species—for instance, *Cymindis humeralis,* in addition to *Brachynus* and *Agonum dorsale*—which often cluster together in the gradient apparatus, must interfere with the fortuitous distribution.

It is always risky to treat biological manifestations purely mathematical as numbers. But these are only symbols whose true content is all too easily forgotten during such studies.

After these remarks on the principles we will now proceed to the report on the experiments conducted. The information given below with each experiment may to some extent appear trivial and inconsequential. But I am of the view that the primary material presented should always be so complete that it can be objectively tested by other researchers. In this way it is possible to discover

sources of error overlooked by the author, or eventually to utilize the material for quite different purposes.

It is advisable to describe these experiments neither in temporal sequence according to my diary nor in the order in which they are discussed in the text of this book, but to arrange them alphabetically by species for each group of experiments.

With each experiment an indication is given of the place where it is discussed in the text. Of course, the text also contains pointers in the opposite direction, to the transcript of experiments.

The number of "specimens" cited for the experiments indicates the cases observed (even if the same individual was utilized more than once).

With few exceptions only those experiments are described whose results are utilized in this book. The results obtained are given only in the running text, and not in the transcript of experiments.

66 A. PREFERENDA EXPERIMENTS

As the name indicates, in these experiments the animal is given freedom of choice among various factors or among various gradations of the same factor.

At the outset attention must be drawn to the fact that the *preferendum* must not be automatically equated with the *optimum.* For instance, it is quite possible that the preferred temperature is not the one at which the life functions of the animal, such as reproduction and development, are optimal. On the other hand a *large* difference between these two "points" is not to be expected, since it would be inappropriate (nonadaptive)—with the exception of the theoretically conceivable case where the animal never came across its preferendum in nature. If a distinct difference between the preferendum and the optimum is to be experimentally detected, it should be established whether this has not resulted from an abnormal situation in the experiment or under the influence of some factor that was overlooked, before the results are attributed to nature. The noteworthy exceptions, such as the strong attractive—usually disturbing—effect of light on nocturnal flying insects, are to be considered as "unnatural situations" (Mast, 1911, pp. 227, 237 ff.).

I. Temperature Gradient Apparatus
("Temperaturorgel")

This device, which has become the most important aid for experimental ecology, was developed by Herter (1924, pp. 225 ff.). It consists of an elongated glass box with a metal floor (copper in my device). The cover has any desired number of holes through each of which a thermometer is inserted so

that the bulb touches the floor. I have used this simple original form of the temperature gradient apparatus (Fig. 3).

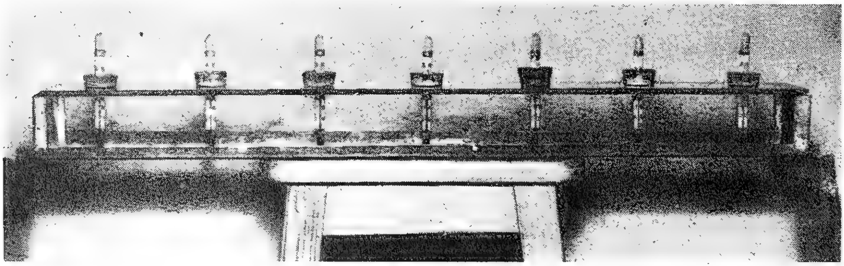
Many investigators have devised modifications of this apparatus in one form or another, including Herter himself (1934; 1939, p. 744). He fitted the bulb of the thermometer into the metal base so that only the temperature of the floor is measured and not that of the air (or of both combined).

I used the original simple type because I was interested in *comparative*, not
67 absolute values. It seemed to me indifferent whether I measured the temperature of the floor or of the air. It is a matter for discussion whether animals always respond more to the temperature of the soil than to that of the air (compare, for instance, Thomsen and Thomsen, 1937, p. 346). If the underneath of the bulb is spherical, as in my experiments, so that it touches the floor only at a point, the readings actually show the temperature of the air next to the floor (not of the floor itself). A particle of sawdust interpolated between the thermometer and the floor, slightly separating the two, caused not the slightest change in the temperature.

The metal floor was sticking out of the box and bent down at both ends into glass beakers, of which one was full of water and warmed by an adjustable spirit lamp and the other was filled with running cold water. On the hottest summer days ice had to be used for cooling. The difference of temperature over the entire apparatus was 20–30°C.

The duration of exposure was about 2 hours (only in Experiment 28 was it considerably less). The location of each insect was not recorded mechanically after a stipulated period but only after it had come to rest. Hence it often happened that the individuals were not all recorded at the same time (but in any case they would be within half an hour).

The main source of error in my temperature gradient apparatus experiments was undoubtedly the *humidity of the air* (cf. also Bodenheimer,
68 1931, and Palmén and Suomalainen, 1945, pp. 38 ff.). It is impossible to maintain the humidity uniform throughout the apparatus without specialized



67 Fig. 3. Temperature gradient apparatus. Floor measurement 7 × 70 cm.

appliances. At the warm end the relative humidity goes down. If one places a moist swab of cotton at the warm end and a water absorbent (for instance, H_2SO_4) at the cold end the preferendum of the animals markedly increases. Their choice of temperature is therefore not a function of their sensitivity to temperature alone. The largest variations are observed in pronouncedly hygrophilous species. In these species, it is sometimes impossible to prevent clustering at that cold end without making the above arrangement for uniform humidity.

However, even if it is possible to maintain the relative humidity throughout the apparatus at 100%, the use of H_2SO_4 cannot prevent the condensation of very fine droplets of water on the wall at the cold end (at least when the temperature there drops below +10°C). This can attract the animals to drink. Besides, a moist floor offers *mechanical* advantages, greatly increasing the adhesive capacity of the tarsi. At least I could not otherwise explain the great difference between the two experiments with *Badister unipustulatus* (Diagram 12; Experiment 5, p. 70). In both cases the air was moisture-saturated throughout the apparatus whereas its floor was first covered with dry sawdust and afterwards with wet sawdust.

These serious sources of error with regard to the humidity enjoin extreme caution in judging that the *absolute* temperature preferendum of a particular species has been determined. This is less consequential for my modest goal of *comparative values*. But care must be taken to handle the species compared
69 in an identical way in the gradient apparatus; the best of all is to carry out a common experiment with both species.

The responses of the animals when they find themselves outside their "preferred zone" in the gradient apparatus differ according to which side of it they are. The warm part causes an immediate strong escape response, and the animal usually hurries back to the cold end without resting. On the other hand, a long stay at the cold end leads to fairly complete torpid, and if the animal is able to reach its preferred zone at all it does so very slowly. The result is a clustering at the cold end and thus a decline in the average preferendum,

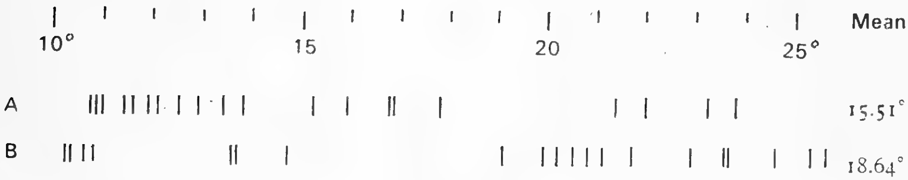


Diagram 12. *Badister unipustulatus.* Temperature gradient apparatus. A—with dry; B—with wet sawdust on floor. Moisture-saturated air in both cases. Experiment 5, p. 70.

especially in more or less hygrophilous species (cf. p. 64 above).

If the group of torpid specimens at the cold end of the apparatus was separated by a distinct gap from the main group of animals in the preferred zone, and looked "unnatural," I changed the approach. I aimed a small lamp at the animals until they became active and sought a new place within the preferred zone. I am of course aware that this eventually raised even the "true" preferendum value. However, the treatment was always identical for both (or all) the species compared, except in the cases recorded below in the transcript of experiments. In more or less xerophilous species the preferred zone is clear and well-defined without any interference (even without wet cotton and H_2SO_4).

Uniform illumination of the temperature gradient apparatus is necessary in the case of species that shun the light, or the animals will usually cluster in the dark corners of the apparatus. All experiments were therefore carried out in darkness or in uniform dim artificial light.

For further literature concerning the temperature gradient apparatus experiments, reference may be made to Herter (1939) and Heerdt (1946).

Concerning the species of *Harpalus*, see Diagram 19 (p. 129).

Experiment 1. Agonum dorsale. Diagram 9, 11, p. 60.

a) May 2, 1945. Gtl. Hörsne, April 29, 1945. 20 specimens. Room temperature 17.5°C. Thermometer readings: 8.0, 11.5, 13.9, 16.6, 19.2, 22.3, 26.9°C.

b) August 24, 1946. Ögl Mogata, August 17–18, 1946. 20 specimens. Room temperature 22.0–22.2°C. Thermometer readings: 12.8, 17.0, 20.2, 23.1, 26.6, 31.6, 39.1°C.

c) July 5, 1947. Öld Halltorp area. June 12–23, 1947. 15 specimens. (together with *Brachynus*). Room temperature about 28°C. Moist cotton at warm end. Lamp at cold end. Thermometer readings: 16.8, 19.5, 22.6, 25.1, 27.8, 31.2, 38.0°C.

d) Same as (c). Room temperature about 27°C. Thermometer readings: 15.4, 19.0, 22.5, 25.2, 28.5, 32.6, 41.0°C.

70 *Experiment 2. Agonum lugens.* July 13, 1947. Upl Sigtuna, July 13, 1947. 20 specimens. Moist cotton at warm end. Room temperature 22°C. Thermometer readings: 10.8, 14.4, 17.2, 20.1, 23.3, 27.9, 35.5°C. Diagram 48, p. 457.

Experiment 3. Agonum viduum. June 25, 1946. Upl Ängby, Rockstasjön Lake, May 26, 1946. 30 specimens. Moist cotton at warm end. Room temperature 22–23°C. Thermometer readings: 9.1, 13.0, 16.5, 19.4, 22.6, 26.8, 33.5°C. Diagram 48, p. 457.

Experiment 4. Badister dilatatus. June 20, 1946. Öld Halltorp, June 11–12, 1946. 20 specimens (together with *B. unipustulatus*). Moist cotton at warm end, very thin layer of wet sawdust on floor. Room temperature 20.4–20.5°C. Thermometer readings: 11.0, 14.7, 17.8, 20.3, 23.6, 28.5, 35.0°C. Diagram 48, p. 457.

Experiment 5. Badister unipustulatus.

a) June 20, 1946. Öld Halltorp. June 11–12, 1946. 20 specimens. Moist

cotton at warm end, few dry sawdust particles on floor. Room temperature about 20.5°C. Thermometer readings: 12.0, 15.4, 18.5, 21.0, 24.8, 30.4, 39.0°C. Diagram 12, p. 68.

b) Same as Experiment 4. Same 20 specimens. Diagrams 12, 48, p. 457.

Experiment 6. Brachynus crepitans. Diagrams 9, 11, p. 60.

a) August 25, 1945. Upl Lovön, April 2, 1945 (i.e. after $4\frac{3}{4}$ months in captivity). 30 specimens. Room temperature 22–23°C. Thermometer readings: 10.2, 15.2, 19.3, 22.6, 26.9, 31.4, 38.6°C.

b) August 26, 1945. Upl Lovön, August 23, 1945. 30 specimens. Room temperature 22.6–22.7°C. Thermometer readings: 12.2, 16.2, 19.6, 22.6, 26.5, 31.2, 38.9°C.

c) August 24, 1946. Upl Lovön, August 23, 1946. 20 specimens. Room temperature 22°C. Thermometer readings: 13.9, 17.2, 20.2, 22.7, 26.1, 31.1, 37.9°C.

d) Same as 1c. 15 specimens (together with *Agonum dorsale*).

e) Same as 1d. 15 specimens.

Experiment 7. Bradycellus collaris, macropterous form and brachypterous form from same population. Jtl Revsund, collected on August 31, 1947. Lamp at cold end. Diagram 46, p. 359.

a) September 5, 1947. Macropterous form. 30 specimens. Room temperature about 23°C. Thermometer readings: 10.1, 14.3, 17.4, 20.5, 24.2, 28.9, 35.7°C.

b) Same as (a). Brachypterous form. 30 specimens. Thermometer readings: 10.3, 14.5, 17.5, 20.5, 24.0, 28.8, 36.5°C.

c) September 6, 1947. Macropterous form [same animals as in (a)]. 30 specimens. Room temperature 24°C. Thermometer readings: 12.0, 15.6, 18.5, 21.4, 24.8, 29.8, 37.5°C.

d) Same as (c). Brachypterous form [same animals as in (b)]. 30 specimens. Thermometer readings: 11.5, 15.4, 18.7, 21.6, 25.5, 31.0, 39.5°C.

Experiment 8. Cymindis angularis. June 25, 1946. Öld Greby, June 11–15, 1946. 14 specimens. Room temperature 23.0–23.2°C. Thermometer readings: 14.2, 17.9, 21.2, 24.6, 27.2, 32.0, 39.9°C. Moist cotton at warm end. Diagram 24, p. 138.

Experiment 9. Cymindis humeralis. June 22, 1946. Öld Greby, June 11–15, 1946. 20 specimens. Room temperature 22.8–23.1°C. Thermometer readings: 13.8, 16.9, 20.1, 22.6, 26.1, 30.6, 37.4°C. Diagram 24, p. 138.

Experiment 10. Cymindis macularis. June 22, 1946. Öld Stora-Rör, June 13, 1946. 20 specimens. Room temperature 22.9–23.6°C. Thermometer readings: 13.9, 17.4, 20.7, 23.3, 27.1, 31.9, 39.6°. Diagram 24, p. 138.

71 *Experiment 11. Harpalus aeneus.* June 23, 1946. Öld Greby, June 11–15, 1946. 20 specimens. Room temperature 24°C. Thermometer readings: 13.9, 16.7, 20.4, 23.5, 27.5, 32.8°C (not read).

Experiment 12. Harpalus anxius. June 21, 1946. Öld Stora-Rör, June 13, 1946. 20 specimens. Room temperature 21.5°C. Thermometer readings: 12.8,

15.9, 18.8, 21.6, 25.1, 30.2, 38.6°C.

Experiment 13. Harpalus azureus. June 21, 1946. Öld Greby, June 11–15, 1946. 20 specimens (all brachypterous). Room temperature 21.5°C. Thermometer readings: 12.8, 16.0, 18.9, 21.6, 25.1, 29.8, 37.7°C.

Experiment 14. Harpalus hirtipes. June 24, 1946. Öld Stora-Rör, June 13, 1946. 15 specimens. Room temperature 22.2–22.6°C. Thermometer readings: 13.6, 16.8, 20.1, 22.9, 26.9, 31.9, 40.2°C.

Experiment 15. Harpalus melleti.

a) May 5, 1945. Gtl Visby, April 28–30, 1945. 20 specimens. Room temperature 18°C. Thermometer readings: 9.0, 13.5, 16.3, 19.3, 23.3, 27.5, 36.1°C. Diagram 7, p. 57.

b) June 25, 1946. Gtl Visby, June 17, 1946. 20 specimens. Room temperature 23°C. Thermometer readings: 13.1, 16.9, 20.2, 23.2, 26.9, 31.8, 38.0°C.

Experiment 16. Harpalus neglectus. June 24, 1946, Öld Stora-Rör, June 13, 1946. 15 specimens. Room temperature 22.5°C. Thermometer readings: 14.0, 17.0, 20.2, 23.1, 27.0, 32.0, 40.7°C.

Experiment 17. Harpalus punctatulus.

a) May 3, 1945. Gtl Visby, April 28, 1945. 19 specimens (in addition one specimen had lost one antenna and showed aberrant behavior). Room temperature 17.3°C. Thermometer readings: 10.5, 14.2, 16.9, 19.1, 22.3, 26.7, 32.1°C. Diagram 6, p. 56.

b) August 26, 1945. Material same as in a) (i.e. after 4 months in captivity). 17 specimens (preference of 5 specimens laying torpid at the cold end was later determined in repeat Experiment 23b together with *H. serripes,* where it was again found to be lower than for the remaining individuals). Room temperature 22.6–22.7°C. Thermometer readings: 14.5, 17.8, 21.0, 23.9, 27.4, 31.5, 38.5°C. Diagram 6, p. 56.

c) June 25, 1946. Gtl Visby, June 17, 1946. 20 specimens. Room temperature 23.0–23.2°C. Thermometer readings: 14.0, 17.4, 20.6, 23.6, 27.6, 32.5, 38.8°C.

Experiment 18. Harpalus puncticeps. June 25, 1946. Öld Halltorp, June 15, 1946. 13 specimens (together with *H. rufitarsis*). Room temperature 23.0–23.5°C. Thermometer readings: 11.8, 15.9, 19.4, 22.2, 25.7, 29.9, 36.1°C.

Experiment 19. Harpalus rubripes. June 22, 1946. Öld Greby, June 11–15, 1946. 20 specimens. Room temperature 23.1–23.2°C. Thermometer readings: 13.9, 17.0, 20.2, 22.7, 25.9, 30.4, 37.1°C.

Experiment 20. Harpalus rufitarsis.

a) Same as Experiment 18. Öld Stora-Rör, June 13, 1946. 7 specimens. Diagram 19, p. 129.

b) June 25, 1946. Same animals as above. Room temperature: 23.1–23.4°C. Thermometer readings: 12.0, 16.3, 20.0, 23.0, 27.2, 32.8, 40.3°C.

Experiment 21. Harpalus rupicola.

a) May 4, 1945. Gtl Visby, April 28–30, 1945. 20 specimens. Room temperature 17.1°C. Thermometer readings: 8.8, 12.4, 15.0, 18.0, 21.9, 27.3, 34.1°C.

Diagram 7, p. 57.

72 b) June 22, 1946. Gtl Visby, June 17, 1946. 20 specimens. Room temperature 22.5–22.9°C. Thermometer readings: 11.6, 15.1, 18.5, 21.3, 24.5, 28.7, 34.2°C.

Experiment 22. Harpalus seladon. May 3, 1945. Gtl Visby, April 30, 1945. 20 specimens. Room temperature 17.9°C. Thermometer readings: 9.1, 12.6, 15.2, 17.9, 21.3, 26.0, 32.4°C.

Experiment 23. Harpalus serripes.

a) May 2, 1945. Gtl Visby, April 29, 1945. 20 specimens. Room temperature 17.9°C. Thermometer readings: 8.7, 11.9, 14.7, 17.6, 21.4, 26.3, 32.5°C. Diagram 5, p. 55.

b) August 26, 1945. Same animals as above (i.e. after 4 months in captivity; together with 5 specimens of *H. punctatulus,* see Experiment 17b). 20 specimens (H_2SO_4 at cold end, which certainly had no influence on this extremely xerophilous animal). Room temperature 22.1–22.6°C. Thermometer readings: 12.4, 16.6, 20.1, 23.1, 27.3, 32.3, 40.2°C.

c) June 28, 1946. Same animals as above (i.e. after 14 months in captivity). 12 specimens. Room temperature about 21.5°C. Thermometer readings: 13.0, 16.0, 19.1, 21.8, 25.4, 30.5, 36.5°C. Diagram 5, p. 55.

Experiment 24. Harpalus smaragdinus. June 23, 1946. Öld Stora-Rör, June 13, 1946. 20 specimens. Room temperature 24.1–24.4°C. Thermometer readings: 15.0, 18.1, 21.7, 24.3, 28.1, 32.8, 39.5°C.

Experiment 25. Harpalus tardus. June 22, 1946. Öland and Gotland, June 12–17, 1946. 20 specimens. Room temperature 22.7–22.8°C. Thermometer readings: 11.1, 15.3, 18.8, 21.7, 25.3, 29.3, 36.9°C.

Experiment 26. Pterostichus anthracinus.

a) April 10, 1945. Upl Djursholm. Ekebysjön lake, April 10, 1945. 17 specimens (6 macropterous specimens, 11 brachypterous specimens). Room temperature 18°C. Thermometer readings: 10.1, 13.0, 15.2, 17.6, 20.1, 23.4, 28.9°C. Diagrams 1, 4, pp. 51, 55.

b) September 1, 1945. F_1 generation obtained by crossing animals in Experiment 26a (emerged on July 4–17, 1945; reared in room from eggs). 15 macropterous, 15 brachypterous specimens, the latter marked with zinc white. Room temperature 21.2–22.0°C. Thermometer readings: 12.8, 16.8, 19.7, 22.4, 26.2, 31.1, 37.1°C. Diagrams 4, 43, pp. 55, 356.

c) Same as b). September 2, 1945. 10 specimens each. Room temperature 21.2–21.5°C. Thermometer readings: 13.0, 17.1, 20.5, 23.3, 27.7, 33.6, 42.1°C. Diagrams 4, 43, pp. 55, 356.

d) Same as b). September 16, 1945. 13 specimens each. Moist cotton at warm end. Room temperature about 19°C. Thermometer readings: 11.5, 14.7, 17.2, 19.8, 23.4, 28.6, 31.5°C. Diagram 43, p. 356.

Experiment 27. Pterostichus nigrita. April 23, 1945. Upl Danderyd, Nora, April 22, 1945. 19 specimens. Room temperature 16.5°C. Thermometer readings: 7.0, 10.6, 12.9, 15.7, 18.4, 22.1, 27.4°C. Diagram 1, p. 51.

Experiment 28. Pterostichus nigrita. May 9–10, 1945. Upl Danderyd, Nora, April 22, 1945. 15 specimens (same animals as in Experiment 27), all individually marked with zinc white. Room temperature 16.8–19.1°C. In 10 experiments (3 on May 9, 7 on May 10), individual *sequence* of animals was recorded (but not temperature) as soon as they came to rest. Exposure between $\frac{1}{2}$ hr and more than 2 hrs. Diagram 2, p. 51.

73 **II. Substratum Gradient Apparatus ("Substratorgel")**

This name here designates the apparatus (Fig. 4) developed by Krogerus (1939, p. 1230) which is here briefly described. The design, which he later modified, is a zinc box (80 × 8 × 8 cm) which contains a series of small zinc boxes of 7.5^3 cm (hence about 400 cm^3), standing next to each other. The upper two-thirds of the juxtaposed sides of the boxes are perforated with big holes, so that the insects can move freely not only along the surface of the box, usually half-filled with substratum, but also in the substratum itself through the boxes. A fine-mesh metal wire gauze was used as cover. Time of exposure 1–2 days.

The experiments were conducted partly as *serial experiments*, i.e. with a smooth gradation of one factor from one end of the gradient apparatus down to the other, and partly as *alternating experiments*, in which only two or three (quantitative or qualitative) different kinds of substrate† were used, mostly in regularly alternating boxes.

The main source of error in these experiments is the tendency of the animals to gather more densely in the boxes at the two ends, partly because further movement is impeded and partly because darker hiding places are easily found there. Hence one must try to provide uniform illumination in the
74 apparatus. This difficulty does not appear in "alternating experiments," since each end of the apparatus has a box containing each of the two substrata. In "serial experiments" it can be compensated at least partly by eliminating the end boxes from the experiment and if necessary by filling these with a substratum having a strong negative influence (i.e. dry or wet sawdust respectively for hygrophilous or xerophilous species). A circular gradient apparatus would perhaps have been better, but here again the method used can be judged as sufficient for the desired *comparative values* (of two or more species).

In order to study, at least in one case, the distribution of animals in the substratum gradient apparatus *without the influence of experimental error,*

†[In this case the apparatus is also called substrate (or substratum) choice apparatus; suppl. scient. edit.].

I made a control experiment with *Amara ingenua* (Diagram 13, Experiment 107, p. 85) for which all the boxes were filled with the same kind of soil. The experiment disturbing clustering of individuals at the two ends of the apparatus was evident.

It would now be possible to correct the figures obtained in different serial experiments (in the case of alternating experiments no control experiment is necessary) from the values given in Diagram 13. I faced the same problem with the "universal gradient apparatus" (p. 85) and found that in this case an empirical correction curve must be plotted for every species. However, apart from the huge amount of work required for this, every factor in an experiment clearly influencing the animals, might not indeed eliminate the above mentioned source of error, but might reduce it to such an extent that a correction of this kind would be too difficult.

I have tried to avoid these difficulties—as far as possible—in realizing

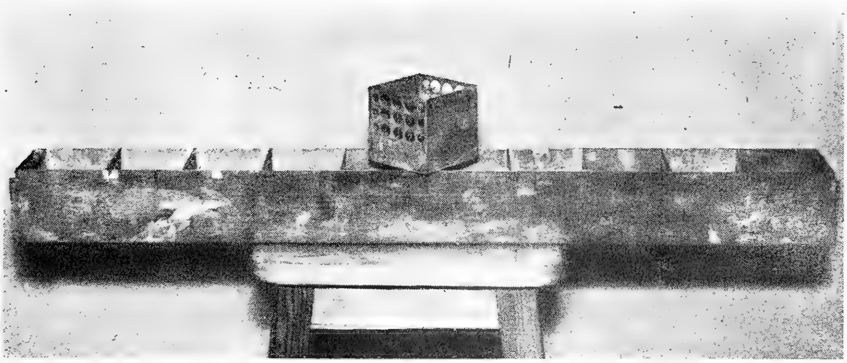


Fig. 4. Substratum gradient apparatus (Krogerus model). 80 × 8 × 8 cm.

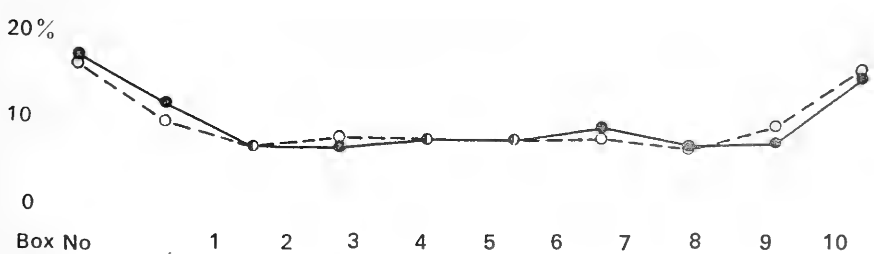


Diagram 13. *Amara ingenua.* Distribution of 200 specimens in the substratum gradient apparatus without influence of any measurable factors. Continuous line—Empirical curve; broken line—Symmetrically *leveled* curve. Experiment 107, p. 85.

alternating experiments (so that the preceding serial experiments served the purpose to determine only the desired quantities of the factors to be examined), or ignoring the end boxes in the experiment (with few exceptions). The exact procedure is given with the description of each experiment below.

In studying some of the smallest species (*Bembidion, Dyschirius*) I had to use other arrangements since the animals were able to crawl into the interstices between the boxes of the substratum gradient apparatus. These experiments are described below in detail (Experiments 92 ff., 95 ff.).

In one case (Experiments 82, 83) the circular universal gradient apparatus (p. 93) was used for a simple substratum experiment (humidity).

a. Serial experiments with $CaCO_3$

Limestone-free, washed, fairly coarse siliceous sand was mixed with $CaCO_3$ (precipitated chalk) in the following series:

Box	1	2	3	4	5	6	7	8	9	10
Sand, cm^3	200	199.61	199.22	198.44	196.88	193.75	187.5	175	150	100
Limestone, cm^3	–	0.39	0.78	1.56	3.13	6.25	12.5	25	50	100

The two mixtures in boxes 2 and 3 were used only in Experiment 29.
Exposure 2 days.
For the species of *Harpalus,* see Tables 2–3 (pp. 121, 122).

*Experiment 29. Brachynus crepitans.**

a) April 10, 1945. Upl Lovön, April 2, 1945, 50 specimens. To each box 25 cm^3 of spring water was added.

b) Same as a). April 12, 1945.

c) Same as a). April 14, 1945.

*Experiment 30. Brachynus crepitans.**

a) Material and method of experiment as in Experiment 29, but to each box CO_2-saturated water (15 cm^3) was added. April 16 through 18, 1945. 50 specimens.

b) Same as a). April 23, 1945.

Experiment 31. Harpalus melleti. May 4, 1945. Gtl Visby, April 28–30, 1945. 24 specimens. Only 8 experimental boxes (Nos. 2 and 3 above excluded), the end boxes had dry sawdust. In each box 20 cm^3 distilled water was added.

76 *Experiment 32. Harpalus melleti.* May 19, 1945. Material and method of experiment as in Experiment 31, but with addition of 10 cm^3 CO_2-saturated water in every box.

Experiment 33. Harpalus punctatulus. May 10, 1945. Gtl Visby, April 28, 1945. 24 specimens. As in Experiment 31, but end boxes had wet humus.

*Limestone was found to have no influence.

Experiment 34. Harpalus punctatulus. May 14, 1945. Material and method of experiment as in Experiment 33, but with 10 cm³ CO_2-saturated water added in every box.

Experiment 35. Harpalus rupicola. May 2, 1945. Gtl Visby, April 28–30, 1945. 24 specimens. As in Experiment 31.

Experiment 36. Harpalus rupicola. May 24, 1945. Material and method of experiment as in Experiment 35, but with 10 cm³ CO_2-saturated water added to each box.

Experiment 37. Harpalus seladon. May 12, 1945. Gtl Visby, April 30, 1945. 24 specimens. As in Experiment 33.

Experiment 38. Harpalus seladon. May 21, 1945. Material and method of experiment as in Experiment 37, but with 10 cm³ CO_2-saturated water added to each box.

Experiment 39. Harpalus serripes.

a) May 6, 1945. Gtl Visby, April 29, 1945. 23 specimens. As in Experiment 31.

b) As in a), but with wet humus instead of sawdust in the end boxes. May 8, 1945.

Experiment 40. Harpalus serripes. May 16, 1945. 21 specimens. Material and method of experiment as in Experiment 39b, but with 10 cm³ CO_2-saturated water added to each box.

b. Alternating experiments at different pH levels

Three substrata were used and their pH determined electrometrically.

1. Soil with humus from the locality of *Harpalus seladon.* Gtl Visby (April 30, 1945), pH 7.5.

2. Soil with humus from the locality of *Pterostichus anthracinus,* Upl Djursholm, Ekebysjön lake (April 10, 1945), pH 4.8.

3. Mixture of 1 and 2, hence with pH of about 6.

Only 7 boxes were used and, with the exception of Experiment 43b, arranged as follows:

Sawdust; pH 6; pH 7.5; pH 6; pH 4.8; pH 6; sawdust.

The moisture of the "pH boxes" was regulated with distilled water. Exposure 2 days.

Concerning the species of *Harpalus,* see Table 4 (p. 124).

Experiment 41. Harpalus melleti. May 14, 1945. Gtl Visby, April 28–30, 1945. 25 specimens. End boxes with wet sawdust.

Experiment 42. Harpalus punctatulus.

a) May 6, 1945. Gtl Visby, April 28, 1945. 25 specimens. End boxes with dry sawdust.

b) Same as a), but with wet sawdust in the end boxes. May 8, 1945.

77 *Experiment 43. Harpalus rupicola.*

a) May 12, 1945. Gtl Visby, April 28–30, 1945. 25 specimens. End boxes with wet sawdust.

b) Same as a), but with a different sequence of pH boxes: 7.5, 6.0, 6.0, 6.0, 4.8. May 16, 1945. 23 specimens.

Experiment 44. Harpalus seladon. May 4, 1945. Gtl Visby, April 30, 1945. 25 specimens. End boxes with dry sawdust.

Experiment 45. Harpalus serripes. May 10, 1945. Gtl Visby, April 29, 1945. 23 specimens. End boxes with wet sawdust.

Experiment 46. Pterostichus anthracinus. August 26 through September 9, 1945. F_1 generation obtained by crossing the animals in Experiment 26a (i.e. from one and the same population) (emergence of adults on July 4–17, 1945; maintained from the egg onward in the room with the substratum pH 4.8). 12 macropterous and 14 brachypterous specimens tested simultaneously, the latter marked with zinc white; and boxes with dry sawdust. The experiment was repeated 5 times, altogether 39 + 39 specimens. Exposure 2 days in each case. Table 28, p. 357.

c. Alternating experiments with limestone gravel and siliceous gravel

The *limestone* was weathered gray gravel from Gtl Visby and the *silicate* was limestone-free diluvial gravel from Upl Djursholm. Particles larger than 4 mm or smaller than 3/4 mm were removed by double filtration and by washing. Medium-size (1–2 mm) particles were somewhat more plentiful in the samples of siliceous gravel. The following difference is noteworthy: The limestone gravel consisted of flat particles, the siliceous gravel of more or less spherical particles. For weight by volume see p. 127.

Only 8 boxes of the substratum gradient apparatus were used. They were almost half-filled (180 cm^3) with the limestone and siliceous gravel alternately. End boxes contained wet sawdust or humus. Moistening (about 10 cm^3 per box) with spring water. Exposure 1 day.

See Table 5 (p. 126).

Experiment 47. Cymindis humeralis. June 21–25, 1946. Öld Greby, June 11–15, 1946. Repeated 4 times, total 100 specimens.

Experiment 48. Harpalus anxius. June 26 through 29, 1946. Öld Stora-Rör, June 13, 1946. Repeated twice, total 100 specimens.

Experiment 49. Harpalus azureus. June 24–29, 1946. Öld Greby, June 11–15, 1946. Repeated 4 times, total 100 specimens.

Experiment 50. Harpalus melleti. July 20 through August 20, 1945. Gtl Visby, April 28–30, 1945. Repeated 5 times, total 100 specimens.

Experiment 51. Harpalus punctatulus. July 12–21, August 18–19, 1945. Gtl Visby, April 28, 1945. Repeated 5 times, total 100 specimens.

Experiment 52. Harpalus rubripes. June 21–24, 1946. Öld Greby, June 11–15, 1946. Repeated 3 times, total 100 specimens.

78 *Experiment 53. Harpalus rufitarsis*. June 26 through July 2, 1946. Öld Stora-Rör, June 13, 1946. Repeated 5 times, total 34 specimens.

Experiment 54. Harpalus rupicola.

a) July 20–26, August 18–20, 1945. Gtl Visby, April 28–30, 1945. Repeated 5 times, total 50 specimens.

b) June 24–26, 1946. Gtl Visby, June 19, 1946. Repeated twice, total 50 specimens.

Experiment 55. Harpalus serripes. July 12–21, August 18–20, 1945. Gtl Visby, April 29, 1945. Repeated 6 times, total 100 specimens.

Experiment 56. Panagaeus bipustulatus. June 26 through July 2, 1946. Öld Greby, June 11–15, 1946. Repeated 5 times, total 39 specimens.

d. Alternating experiments with limestone gravel and schist gravel

Limestone gravel as described above. The *schist gravel* consisted of limestone-free argillaceous slate from Dlr Osmundberget, which was triturated and subjected to filtering and washing, as in the case of limestone. The particles were even flatter than those of limestone. For weight by volume, see p. 128.

Moistening with distilled water. Otherwise exactly as in the preceding series of Experiments 47–56.

See Table 6 (p. 127).

Experiment 57. Harpalus anxius. July 3–9, 1946. Öld Stora-Rör, June 13, 1946. Repeated 5 times, total 100 specimens.

Experiment 58. Harpalus azureus. July 2–16, 1946. Öld Greby, June 11–15, 1946. Repeated 7 times, total 100 specimens.

Experiment 59. Harpalus melleti. July 3–16, 1946. Gtl Visby, June 19, 1946. Repeated 6 times, total 100 specimens.

Experiment 60. Harpalus rufitarsis. July 2–14, 1946. Öld Stora-Rör, June 13, 1946. Repeated 5 times, total 35 specimens.

Experiment 61. Harpalus rupicola. July 2–15, 1946. Gtl Visby, June 18, 1946. Repeated 6 times, total 100 specimens.

Experiment 62. Panagaeus bipustulatus. July 3–9, 1946. Öld Greby, June 11–15, 1946. Repeated 5 times, total 34 specimens.

e. Serial experiments with variable humidity

Only 7 boxes were used (6 in Experiment 81). In each of these, a different quantity of water was added to 200 cc of dry sawdust (of aspen poplar) in the following series:

Box	1	2	3	4	5	6	7
H_2O, cc	0	$3\frac{1}{8}$	$6\frac{1}{4}$	$12\frac{1}{2}$	25	50	100

Exposure one day (during spring 2 days) unless otherwise stated (the heat of summer caused a too rapid drying of the sawdust).

79 The experiments with *Harpalus* (and *Cymindis*) were carried out simultaneously using several species, without this being noted in each case.

It should be mentioned that delicate freshly emerged beetles should not be used in these experiments, since they have a demonstrably higher moisture requirement.

Concerning the species of *Harpalus,* see Diagrams 21–22 (p. 133).

Experiment 63. Cymindis angularis. July 3–23, 1946. Öld Greby, June 11–15, 1946. Repeated 4 times, total 40 specimens*.

Experiment 64. Cymindis humeralis. July 18–23, 1946, Öld Greby, June 11–15, 1946. Repeated 3 times, total 60 specimens*.

Experiment 65. Cymindis macularis. July 3–23, 1946. Öld Stora-Rör, June 13, 1946. Repeated 4 times, total 60 specimens.*

Experiment 66. Harpalus aeneus. June 25–27, 1946. Öld Greby, June 11–15, 1946. Repeated twice, total 75 specimens.

Experiment 67. Harpalus anxius. June 28 through July 2, 1946. Öld Stora-Rör, June 13, 1946. Repeated 3 times, total 75 specimens.

Experiment 68. Harpalus azureus. June 23 through July 1, 1946. Öld Greby, June 11–15, 1946. Repeated 3 times, total 75 specimens.

Experiment 69. Harpalus hirtipes. June 25 through July 2, 1946. Öld Stora-Rör, June 13, 1946. Repeated 4 times, total 50 specimens.

Experiment 70. Harpalus melleti.

a) May 19–23, 1945. Gtl Visby, April 28–30, 1945. Exposure 2 days, repeated twice, total 40 specimens.

b) Same as a), but with only one day of exposure. June 23 through July 1, 1946. Gtl Visby, June 17–19, 1946. Repeated 3 times, total 75 specimens.

Experiment 71. Harpalus neglectus. June 25 through July 3, 1946. Öld Stora-Rör, June 13, 1946. Repeated 5 times, total 50 specimens.

Experiment 72. Harpalus punctatulus.

a) May 19–23, 1945. Gtl Visby, April 28, 1945. Exposure 2 days, repeated twice, total 41 specimens. Diagrams 8, 22, pp. 57, 134.

b) Same as a), but with only one day of exposure. June 23 through July 1, 1946. Gtl Visby, June 17, 1946. Repeated 3 times, total 75 specimens. Diagrams 8, 21, pp. 57, 133.

c) Same as b), but before the experiment the animals were kept for 2 days in moisture-saturated air, July 2–3, 1946. 50 specimens. Diagram 8, p. 57.

Experiment 73. Harpalus puncticeps. June 23 through July 3, 1946. Öld Halltorp, June 15, 1946. Repeated 5 times, total 50 specimens.

Experiment 74. Harpalus rubripes. June 28 through July 2, 1946. Öld Greby, June 11–15, 1946. Repeated 3 times, total 75 specimens.

80 *Experiment 75. Harpalus rufitarsis.* July 18–24, 1946. Öld Stora-Rör, June 13, 1946. Repeated 4 times, total 28 specimens.

*The three species of *Cymindis* did not behave distinctly different.

Experiment 76. Harpalus rupicola.

a) May 19–23, 1945. Gtl Visby, April 28–30, 1945. Exposure 2 days, repeated twice, total 42 specimens.

b) Same as a), but with only one day of exposure. June 23 through July 1, 1946. Gtl Visby, June 17, 1946. Repeated 3 times, total 75 specimens.

Experiment 77. Harpalus seladon.

a) May 19–23, 1945. Gtl Visby, April 30, 1945. Exposure 2 days, repeated twice, total 39 specimens.

b) Same as a), but with only one day of exposure. August 24–27, 1946. Öld Greby, June 11–16, 1946. Repeated twice, total 100 specimens.

Experiment 78. Harpalus serripes.

a) May 19–23, 1945. Gtl Visby, April 29, 1945. Exposure 2 days, repeated twice, total 42 specimens.

b) Same as a), but with only one day of exposure. June 25 through July 2, 1946. Öld Greby, June 11 through 15, 1946. Repeated 6 times, total 150 specimens.

Experiment 79. Harpalus smaragdinus. June 25–28, 1946. Öld Stora-Rör, June 13, 1946. Repeated 3 times, total 75 specimens.

Experiment 80. Harpalus tardus. June 25–28, 1946. Öld and Gtl., June 14–18, 1946. Repeated 3 times, total 75 specimens.

Experiment 81. Pterostichus anthracinus. September 16 through October 1, 1945. F_1 generation obtained by crossing the animals in Experiment 26a (i.e. from one and the same population) (adults emerged from July 4–17, 1945; maintained from the egg onwards in the room in wet humus soil). 13 macropterous and 13 brachypterous specimens simultaneously tested, the former marked with zinc white. 6 boxes (those with 3 1/8 cm^3 water excluded; see p. 78). Exposure one day, repeated 8 times, altogether 100 + 100 specimens. Diagram 44, p. 357.

* * *

Experiment 82. Agonum dorsale. July 8, 1947. Öld Halltorp area, June 12–23, 1947. The experiment was carried out in the circular universal gradient apparatus (p. 93). About 1/2 cm thick layer of sawdust in 20 boxes of 10 moisture gradations (each duplicated as in Experiment 108 ff.). A lamp in the center of the gradient apparatus uniformly illuminated all the boxes. A glass plate was used as cover, through which observations of the beetles were made every 2 hours without touching the gradient apparatus. 40 specimens (including *Brachynus*). 3 replicates, hence total 120 specimens. Diagram 10, p. 61.

Experiment 83. Brachynus crepitans. July 8, 1947. Öld Halltorp area, June 12–23, 1947. As in Experiment 82. 40 specimens (including *Agonum dorsale*). Diagram 10, p. 61.

f. Serial and alternating experiments with salts and ammonia

The purpose of the serial experiments was to determine a possible pre-
81 ferendum to the concentration of substances in question for each species, with which alternating experiments could then be carried out. Coarse siliceous sand was used as neutral substratum.

The experiments with *Amara* were carried out in the usual substratum gradient apparatus (p. 73). In serial experiments all 10 boxes were used with 2 days of exposure. In alternating experiments only six of these were used with one day of exposure (except in Experiment 84b). A different arrangement was adopted only in the ammonia experiment (Experiment 88). See also p. 525.

In the case of the species of *Bembidion* the substratum was placed in a series of 6 small cuvettes (about 100 cm^3), which were placed in a row at the bottom of a large glass container with the broad sides touching each other. The container was filled with water almost to the edge of the cuvettes, and strips of paper placed in the water enabled beetles that fell in to climb out again. Exposure 1 day. See p. 523.

Experiment 84. Amara ingenua.

a) Serial experiment with $Ca(NO_3)_2$. September 16–26, 1945. Upl Solna, Bergshamra, September 15, 1945. Each box with 160 cm^3 of sand and 25 cm^3 of liquid in the following sequence:

Box	1	2	3	4	5	6	7	8	9	10
Salt solution	Distilled water	1/4%	1/2%	1%	2%	3%	4%	5%	7½%	10%

Repeated 4 times, total 100 specimens.

b) Alternating experiment with $Ca(NO_3)_2$. October 23 through November 2, 1945. The same animals as above. 6 boxes, alternately with distilled water and 5% $Ca(NO_3)_2$ solution. Exposure 2 days. Repeated 3 times, total 66 specimens.

Experiment 85. Amara ingenua. Serial experiment with Thomas phosphate (commercial quality). November 10–14, 1945. Upl Solna, Bergshamra, September 15, 1945. Each box with 160 cm^3 of sand and 25 cm^3 of liquid in the following sequence:

Box	1	2	3	4	5	6	7	8	9	10
Salt solution*	Distilled water	0.08%	0.15%	0.3%	0.63%	1.25%	2.5%	5%	7.50%	10%

Repeated twice, total 44 specimens.

Experiment 86. Amara ingenua.

a) Serial experiment with superphosphate ($7 \cdot Ca(H_2PO_4)_2 + 5 \cdot CaSO_4$). January 27 through February 8, 1946. Upl Solna, Bergshamra, September 15,

*Thomas phosphate is merely suspended in water, but I tried to obtain as uniform a distribution of the particles as possible by shaking.

1945. Each box with 160 cm^3 of sand and 25 cm^3 of liquid in the following sequence:

Box	1	2	3	4	5	6	7	8	9	10
Salt solution	Distilled water	0.25%	0.5%	1%	2%	3%	4%	5%	7.5%	10%

Repeated 4 times, total 72 specimens.

b) Alternating experiment with superphosphate. February 14–18, 1946. The same animals as above. Six boxes, alternately with distilled water and 2% superphosphate solution. Exposure one day. Repeated 4 times, total 72 specimens.

Experiment 87. Amara ingenua.

a) Serial experiment with KCl. December 22–31, 1945. Upl Solna, Bergshamra, September 15, 1945. Each box with 160 cm^3 of sand and 25 cm^3 of liquid in the following sequence:

82 Box	1	2	3	4	5	6	7	8	9	10
Salt solution	Distilled water	1/4%	1/2%	1%	2%	3%	4%	5%	$7\frac{1}{2}$%	10%

Repeated 4 times, total 83 specimens.

b) Alternating experiment with KCl. January 6–15, 1946. The same animals as above. Six boxes alternately with distilled water and 1% KCl solution. One day of exposure. Repeated 5 times, total 109 specimens.

Experiment 88. Amara ingenua.

a) Experiment with ammonia (commercial quality) February 23, 1946. Upl Solna, Bergshamra, September 15, 1945. Six boxes, each with 160 cm^3 of sand and 25 cm^3 of liquid in the following sequence:

Box	1	2	3	4	5	6
Solution	Distilled water	Distilled water	Distilled water	1%	2%	3% ammonia.

17 specimens. Exposure one day.

b) Same as a), but with lower concentration of ammonia. March 3–4, 1946.

Box	1	2	3	4	5	6
Solution	Distilled water	Distilled water	Distilled water	1/8%	1/4%	1/2% ammonia.

15 specimens. Exposure one day.

Experiment 89. Amara praetermissa. Alternating experiment with $Ca(NO_3)_2$. August 24–28, 1946. Upl Djursholm, August 24, 1946. Exactly as in Experiment 84b. Repeated twice, total 100 specimens.

Experiment 90. Amara praetermissa. Alternating experiment with superphosphate ($7 \cdot Ca(H_2PO_4)_2 + 5 \cdot CaSO_4$). September 1–5, 1946. Upl Djursholm, August 24, 1946. Exactly as in Experiment 86b, but exposure 2 days. Repeated twice, total 100 specimens.

Experiment 91. Amara praetermissa. Alternating experiment with KCl. August 28 through September 1, 1946. Upl Djursholm, August 24, 1946. Exactly as in Experiment 87b, but exposure 2 days. Repeated twice, total 100 specimens.

Experiment 92. Bembidion aeneum.

a) Alternating experiment with NaCl (together with *B. minimum*). August 24 through September 4, 1946. Boh Sämstad, August 10, 1946. 6 cuvettes (see p. 81), each with 100 cm^3 of coarse siliceous sand and 15 cm^3 of liquid (alternating spring water and 1% NaCl solution). Exposure one day. Only 5–7 specimens, hence repeated 11 times, total 50 specimens.

b) Same as a). June 25 through July 12, 1947. Öld Möckelmossen, June 18, 1947. Only 5 specimens, so repeated 19 times, total 50 specimens.

Experiment 93. Bembidion minimum.

a) Serial experiment with NaCl. August 20–22, 1946. Boh Sämstad, August 10, 1946. 6 cuvettes (see p. 81), each with 100 cm^3 of coarse siliceous sand and 10 cm^3 of liquid in the following sequence:

Cuvette	1	2	3	4	5	6
Salt solution	Spring water	1/8%	1/4%	1/2%	1%	2% NaCl.

Exposure one day, repeated twice, total 29 specimens.

b) Same as 92a. Alternating experiment with NaCl (together with *B. aeneum*). August 24–31, 1946. Boh Sämstad, August 10, 1946. Repeated 8 times, total 50 specimens.

83 **g. Serial experiments with sand of various particle size**

The sand obtained from "Statens Väginstitut," Stockholm, was divisible into the following six categories:

1) 2.0 to 1.0 mm particle size. Gst Gävle, airfield. Isolated limestone particles (detected with HCl).

2) 1.0 to 0.5 mm = 1.

3) 0.5 to 0.25 mm. Hls Sandarne. Limestone-free.

4) 0.25 to 0.125 mm. Vrm Karlstad, airfield. Limestone-free.

5) 0.125 to 0.075 mm. Mdp Sundsvall, airfield. Limestone-free.

6) < 0.075 mm = 5.

Except for *Dyschirius* (Experiments 95, 96), the usual substratum gradient apparatus was used in all experiments. Six boxes were placed in the container, each with 175 cm^3 of sand of categories 1–6 in simple sequence. See Diagram 51 (p. 506).

For *Dyschirius* a deep dish was used, divided by vertical strips of paper into 6 equal sectors, each with a different type of sand. In this case a circular gradient apparatus was used. See Diagram 52 (p. 507).

Since completely dry sand could not be used, I tried to judge its water-holding capacity, i.e. the "relative" moisture content, as follows: 20 cm^3 of each category of sand was placed in a reagent tube, as tightly packed as possible. Water was carefully added until the air was completely excluded and the water formed about a one mm thick layer on the surface. The quantities of water required for this purpose were:

Category of sand	1	2	3	4	5	6
Water, cm^3	9	9.5	10	9.5	10.5	9.7

According to these proportions different quantities of water were added to the sand, beginning with 5 cm^3 (10 cm^3 in the case of *Dyschirius*) per 100 cm^3 of type 3.

Doubtless it would have been more accurate to determine the moisture preferendum of every species first for each category of sand and then carry out a comparative study of the six samples obtained in this way.

Exposure one day in every case.

Experiment 94. Cymindis macularis. July 24–30, 1946. Öld Stora-Rör, June 13, 1945. Repeated 5 times, total 50 specimens. Irregular distribution of the individuals.

Experiment 95. Dyschirius obscurus. August 18–26. 1947. Nl Tvärminne, around August 1, 1947. Deep dish with 6 different sectors for sand (see above). Repeated 8 times, total 100 specimens.

84 *Experiment 96. Dyschirius thoracicus.* June 20–28, 1947. Öld Hornsjön lake, June 15, 1947. Exactly as in Experiment 95. Repeated 5 times, total 150 specimens (in two experiments, 63 specimens, the moisture content of the sand was checked only with the fingers).

Experiment 97. Harpalus anxius. July 29–30, 1946. Öld Stora-Rör, June 13, 1946. Repeated twice, total 100 specimens.

Experiment 98. Harpalus hirtipes. July 24–29, 1946. Öld Stora-Rör, June 13, 1946. Repeated 5 times, total 75 specimens.

Experiment 99. Harpalus neglectus. July 24–30, 1946. Öld Stora-Rör, June 13, 1946. Repeated 6 times, total 50 specimens.

Experiment 100. Harpalus rufitarsis. July 24–31, 1946. Öld Stora-Rör, June 13, 1946. Repeated 6 times, total 35 specimens.

Experiment 101. Harpalus serripes. July 24–27, 1946. Öld Greby, June 11–15, 1946. Repeated 3 times, total 100 specimens.

Experiment 102. Harpalus smaragdinus. July 28–31, 1946. Öld Stora-Rör, June 13, 1946. Repeated 4 times, total 100 specimens.

Experiment 103. Harpalus tardus. July 28–31, 1946. Öld and Gtl, June 14–18, 1946. Repeated 3 times, total 75 specimens.

h. Experiments on the relationship between two species

The suspected "passive" species was confined within wide-meshed net or wire gauze walls, and the suspected "active" species was left free to settle anywhere, or close to the walls, through which of course the smell of the beetles passed.

Experiment 104. Brachynus crepitans versus *Agonum dorsale.* May 26 through June 1, 1945. Upl Lövon, April 2, 1945 (*Agonum*, Gtl Hörsne, April 29, 1945). 5 boxes of the substratum gradient apparatus (half-filled with sand) were used, the middle one was closed with a thin cloth after releasing 10 specimens of *Agonum* into it. The open boxes contained 24 specimens of *Brachynus*. Exposure for 3 days. Each experiment was repeated 3 times, total 72 specimens of *Brachynus*; p. 549.

Experiment 105. Dyschirius obscurus versus *Bledius arenarius* Payk. August 14–18, 1947. Nl Tvärminne, around August 1, 1947 (both species). Deep dish with humid sand. Two small wire gauze cages (devised by Palmén), 2.5 × 2.5 × 2.5 cm, were placed in the sand exactly opposite one another, close to the edge of the dish (Fig. 5). One contained 6–8 specimens of *Bledius* and the other was empty. The 4 sectors (see figure) were made only the following day during observation, and the distribution of *Dyschirius* in these was recorded. Repeated 4 times, total 50 specimens; p. 546.

Experiment 106. Dyschirius thoracicus versus *Bledius arenarius.* June 18–20, 1947. Öld Hornsjön lake, June 15, 1947 (both species). Exactly as Experiment 105. Repeated twice, the second time with 5 specimens of *Stenus* spp. in the cage that was empty the first time, total 65 specimens; p. 546.

85 **i. Distribution of insects in the substratum gradient apparatus without the influence of determinable factors (control experiment)**

Experiment 107. Amara ingenua. September 29 through October 18, 1945. Upl Solna, Bergshamra, September 15, 1945. All 10 boxes were used, each with 160 cm³ of coarse sand and 25 cm³ of distilled water. Exposure for 2 days. Repeated 9 times, total 200 specimens. Diagram 13, p. 74.

III. The Universal Gradient Apparatus ("Universalorgel")

I have given this pretentious name to an apparatus developed by alterations of Krogerus' substratum gradient apparatus (p. 73). In addition to this "linear" universal gradient apparatus, I have also developed a "circular" one, which is described below in detail, although it proved less suitable for my purpose.

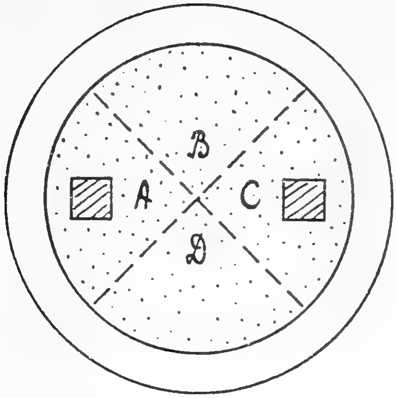


Fig. 5. Circular substratum gradient apparatus (plate) used for studying relationship between *Dyschirius* and *Bledius*. Experiments 105, 106, p. 84. A–C are sectors partitioned when recording observations. Striated squares are small cages of wire gauze. Dotted area—sand.

The principle of the universal gradient apparatus involves study of the simultaneous effects of 2 or more factors (3 in the present case) in various combinations. It is therefore a substratum gradient apparatus which also functions as a temperature gradient apparatus with the help of the bent copper sheets soldered to the ends.

The boxes of the universal gradient apparatus do not have perforated walls as in the substratum gradient apparatus, but are provided with a 5 mm high
86 horizontal slit (Fig. 6), only 5 mm above the bottom, through which animals of that particular size can pass, but which fairly effectively isolates the air contained in the adjacent boxes.

In my experiments, the factors *temperature, humidity* (of the bottom substratum, to a lesser extent that of the air), and *light* were investigated*. Each of these is here treated separately, and the more important experimental errors are pointed out.

Temperature. As in the case of the temperature-gradient apparatus, the copper plate at one end was immersed in water heated by an adjustable spirit lamp, whereas at the other end there was continuous cooling with cold running water. It differs from the usual temperature gradient apparatus in the fact that the position and temperature preferendum of individual animals could not be determined, since these were distributed over 10 temperature categories (= boxes), whose mean temperature must be calculated.

For this purpose two sets of temperature readings were taken for all the boxes at the same temperature of hot and cold running water 50°C and 11.8°C

*The chemical characteristics (for instance, the NaCl content) of the water could easily be considered as a fourth factor.

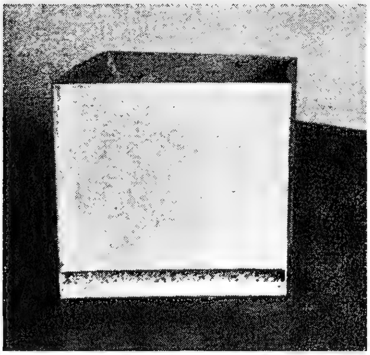


Fig. 6. Box of the (circular) "universal gradient apparatus."

respectively). In one case the bulbs of all the thermometers rested on the
87 bottom against the warmer wall and in the other against the cooler wall of each box. The following figures were recorded:

Box	1	2	3	4	5
Temperature	16.4–17.5	18.6–19.8	20.5–21.2	21.9–22.6	22.7–23.2
Mean	17.0	19.2	20.9	22.3	23.0
Box	6	7	8	9	10
Temperature	23.5–24.0	24.4–24.8	26.0–26.9	27.5–28.4	31.8–33.7
Mean	23.8	24.6	26.5	28.0	32.7

The fall in temperature in the universal gradient apparatus thus occurs by steps, with high levels at the warm end of the apparatus along the edge of the two boxes (Diagram 14). These falls may exercise an interfering, choking effect on the beetles and serve as barriers. The diagram also shows that the temperature plot of the universal gradient apparatus is less uniform than that of the temperature gradient apparatus, because the fall in temperature in the middle parts of the apparatus is smoother. Direct comparison of the preferenda obtained in the two gradient apparatuses is therefore not possible.

88 With a steeper fall in temperature in the universal gradient apparatus, the temperature of the adjacent boxes at both ends of the apparatus differed still more. A simultaneous reading at the warm and cold walls in the three warmest and two coldest boxes provided the following data:

Box	1	2	...	8	9	10
Temperature	14.3–15.3	17.0–18.0	...	27.3–28.8	31.1–34.0	35.4–39.1
Mean	14.8	17.5		28.1	32.6	37.3

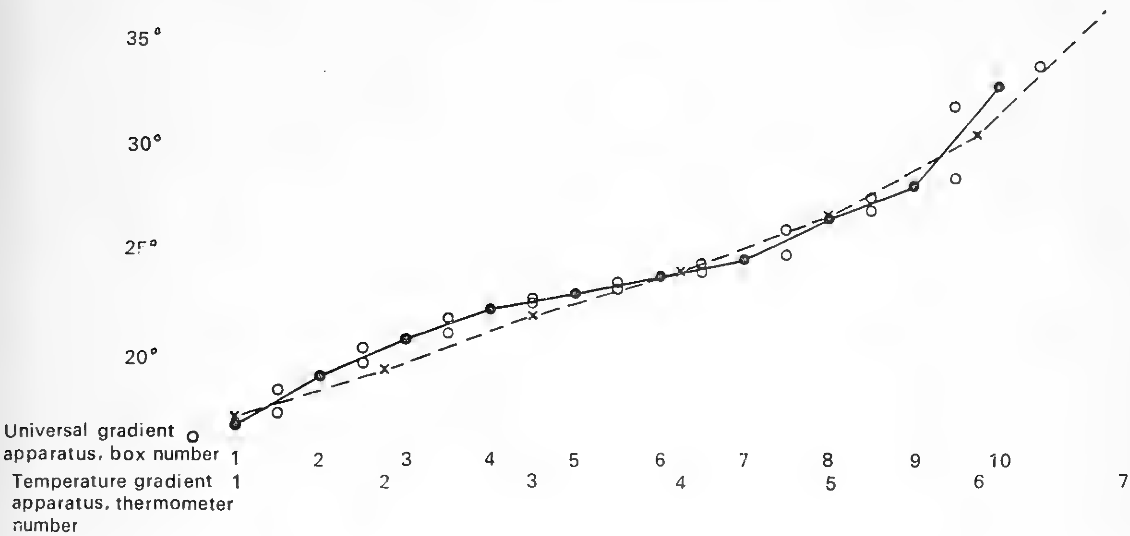


Diagram 14. Comparison between the fall in temperature in the universal gradient apparatus (circles) and in the temperature gradient apparatus (crosses). Open circles—Extreme temperatures; Black circles—Calculated mean value for each box in the universal gradient apparatus.

In all the experiments with beetles the thermometers in the 5 "warm" boxes touched the warm wall and in the 5 "cold" boxes touched the cold wall. The average temperature of every box was estimated from readings so taken.

All measured and estimated temperatures, as in the case of the temperature gradient apparatus (p. 66), are of the layer of air next to the bottom, but not of the bottom itself. Several control experiments, both with dry sawdust and with different grades of moist sawdust, showed that the temperature reading was not dependent upon whether the thermometer directly touched the bottom or not.

Humidity. Every box in all the experiments contained 25 cm^3 of sawdust (of aspen poplar), which was uniformly spread over the bottom in an almost 5 mm thick layer. If the humidity factor was studied simultaneously, different quantities of water were added to the sawdust samples, resulting in the following smoothly ascending series:

Box	1	2	3	4	5	6	7	8	9	10
H_2O, cm^3	0	0.5	1	2	3	4	5	6	8	10

Before carrying out the experiment, water was distributed in each sample as uniformly as possible by careful mixing. One sample was never used in more than two successive experiments.

The differences between these samples lay in the moisture content of the *substrata*, rather than in that of the *air*, which was also taken into consideration when testing species with burrowing habits (only the genus *Harpalus*). However, in order to determine the humidity of the air in the boxes the following measurements were taken with a calibrated hair-hygrometer:

a) Humidity series as above, without temperature differences (room temperature 22.7°C, relative humidity of the air 69%):

Box	1	2	3	4	...	10
Water content of sawdust (H_2O, cm^3)	0	0.5	1	2	...	10
% relative humidity of air	69	84	99		100	

89 b) Simultaneous humidity and temperature series ("warm-dry") (room temperature 25.0°C, relative humidity of the air, 64%):

Box	1	2	3	4	5	6	7	8	9	10
Temperature (mean)	41.9	34.4	31.2	28.0	26.0	24.3	23.0	20.8	17.7	15.2
H_2O, cm^3	0	0.5	1	2	3	4	5	6	8	10
% relative humidity of air	70	92	100	100	100	100	100	100	100	100

c) Inverse humidity and temperature series ("warm-moist") (room temperature 24.7°C, relative humidity of air, 64%):

Box	1	2	3	4	5	6	7	8	9	10
Temperature (mean)	39.5	34.0	30.6	26.6	25.5	23.5	22.9	19.7	17.1	15.7
H_2O, cm^3	10	8	6	5	4	3	2	1	0.5	0
% relative humidity of air	100	100	100	100	100	100	96	90	75	64

d) Temperature data as in b) and c) (38.7–15.2°C) but throughout with dry sawdust (room temperature 22.7°C, relative humidity of the air 69%). The relative humidity of the air in the boxes varied only from 72% at the warm end to 68% at the cold end.

These data show: first, that the relative humidity of the air reaches 100% even with low moisture in the sawdust, and it therefore has a very small influence on the distribution of beetles in the apparatus; second, that the volumes of air in different boxes are apparently well isolated from one another, since adjacent boxes can show for a long period such different percentages of relative humidity of the air as 64, 75, 90 or 70, 92, 100%. The exchange of air through the narrow slit at the bottom of the boxes is evidently very little, which must also be conducive to the maintenance of constant temperature during the experiment.

In experiments where the humidity factor had no importance, dry or almost dry sawdust (2 cm^3 H_2O per 25 cm^3) was used.

Light. Corresponding to each box, four small squares were cut out in thick black opaque paper; the total exposed surface area of the boxes decreased in
90 the following sequence: 1 (without paper, all 55 cm^2 open), 1/2 ($27\frac{1}{2}$ cm^2), 1/4 ($13\frac{3}{4}$ cm^2), . . ., 1/256, 0 (dark). Cf. Fig. 7. The paper, together with a tightly fitting glass lid, formed the cover of the apparatus.

Quantitative measurements of the light entering each box were not taken. They would have been useful only if the same (artificial) source of light was always used, which was not the case. All the "light experiments" were carried out in the same room with indirect daylight, never with a completely overcast sky, from June through early August. Hence the results are in no way precise. However, since light was studied only as a "regulating" factor in relation to temperature and humidity, the procedure might be considered suitable.

All experiments without the light factor were carried out in the dark, using black paper all over.

The experiments with the universal gradient apparatus are also subject to errors other than those mentioned above, some of which affected the experiments on the temperature and substratum gradient apparatus as well (see pp. 66 and 73).

In addition, the following points may be emphasized:

1) The short duration of exposure (always 2 hours). This was necessary when very dry sawdust was used, since this has a harmful effect on the less xerophilous species, and such animals soon become restless.

2) The readings in each experiment were recorded as follows: After removing the lid the boxes were taken as quickly as possible and placed in a porcelain dish whereupon the animals were counted. A certain amount of disturbance, which often drove the faster, "more nervous" species from their resting position into another box, could not be avoided. When a large number of beetles are involved, and one need not take care (as I had to do) that some individuals are not crushed each time, the boxes should be isolated from one another quickly, without removing them, by inserting thin metal plates in between.

3) At high temperatures, on account of the increased loss of water from

the animal, dry sawdust has a stronger negative influence, and therefore the temperature preferendum is higher with moist sawdust. Furthermore, two experiments with dry sawdust must not be carried out in quick succession, because the animals get thirsty and behave abnormally.

4) Because of the slight temperature differences among the boxes *in the*
91 *middle* (see Diagram 14), the beetles are distributed more sparsely there and exhibit less distinct maxima than in the pure temperature gradient apparatus.

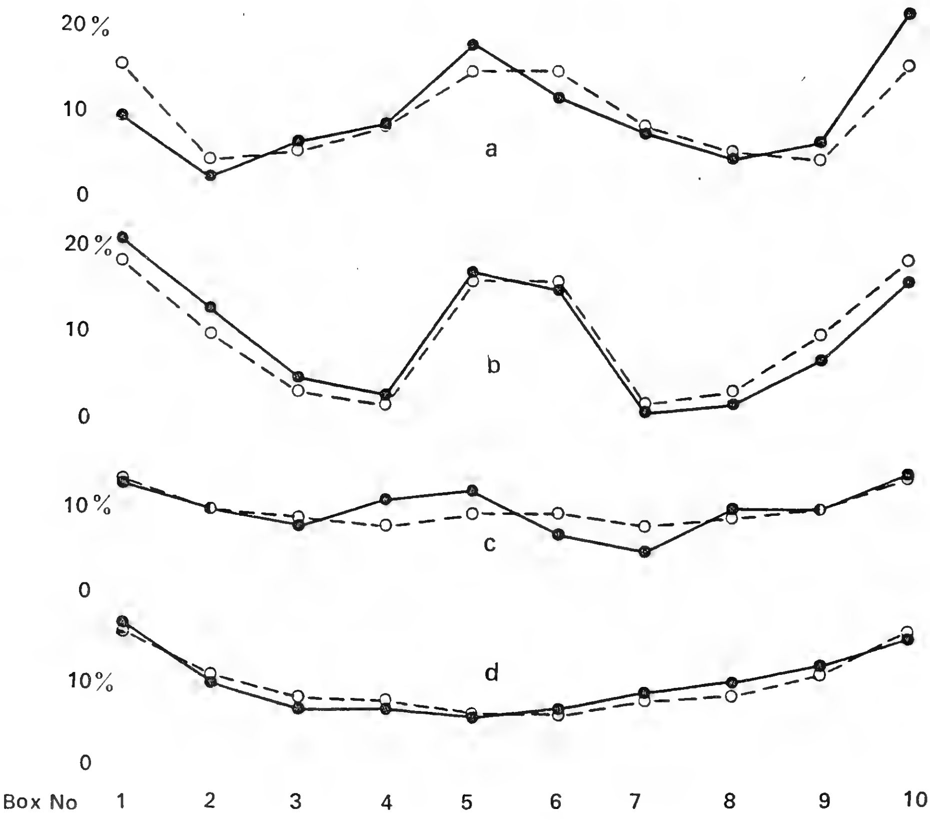


Diagram 15. Distribution of 100 specimens each of given species in the universal gradient apparatus without influence of any measurable factor. a—*Harpalus punctatulus*; b—*H. seladon*; c—*H. melleti*; d—*H. serripes*. Continuous line—Empirical numbers; broken line—Symmetrically leveled numbers. Experiment 119, p. 103.

5) As in the case of the linear gradient apparatus (see p. 73), most species show a tendency to *cluster at the ends*. Since the warm end has a repelling effect, this means that in an experiment where the temperature factor is also involved, over-representation results in the cold part of the gradient apparatus. Besides,
93 (at every temperature), the moist part of the apparatus to a lower extent, slows down the movements of the animals.

As in the case of the substratum gradient apparatus (Diagram 13), some species were investigated, with respect to these errors, i.e. their distribution in the universal gradient apparatus was studied (Diagram 15), *without the influence of measurable factors*. The result is that even species that are taxonomically and ecologically closely related may behave differently in this respect. Evidently correction of the results of the remaining experiments can be undertaken on the basis of these diagrams. An example of how this can be done is provided by the experiment with *Harpalus punctatulus* concerning the "humidity" factor (Diagram 16).

Otherwise I have not made any correction of the experimental values of the four species studied (or any others) (cf. p. 74). The main reason is that the experiments with the universal gradient apparatus were primarily intended to be a study of the *variations* shown by the same species under the influence of various combinations of factors, whereat the correction would be an unimportant constant.

On the other hand, I have tried to avoid this disproportionate distribution in the apparatus by devising a *circular universal gradient apparatus* (Fig. 7). This contains 20 boxes, double the linear apparatus. Unfortunately it was found that taking readings for every experiment (point No. 2 above) with so many boxes resulted in excessive disturbance of the active carabids and I had to give up this apparatus after several trials. However, the apparatus can be useful with slow-moving species and those that do not hide in the ground (or are not studied with respect to the substratum), since the results can be recorded through the glass lid.

Moreover, in the circular gradient apparatus the "unnatural" clustering in the cold part, especially if it was also moist, can be eliminated only in certain cases (Diagram 17); in other cases it was unavoidable (Diagram 18). For my purpose, therefore, the apparatus was no better than the linear arrangement.

In conclusion one might ask, in view of the numerous demonstrable experimental errors and inaccuracies in the results with the universal gradient apparatus, whether it was useful to spend so much time on these experiments. I think it was. In part, the results are not quite in the nature of fortuitous hap-
94 penings, as might have been expected, which was shown by the often remarkable identical distribution of the animals in repeated experiments (Diagrams 25–35, pp. 141 ff.). Then again, as in the case of all the similar experiments included in this book, I am convinced that from the *comparative* values obtained with simultaneous studies on two or more species, certainly no physiological,

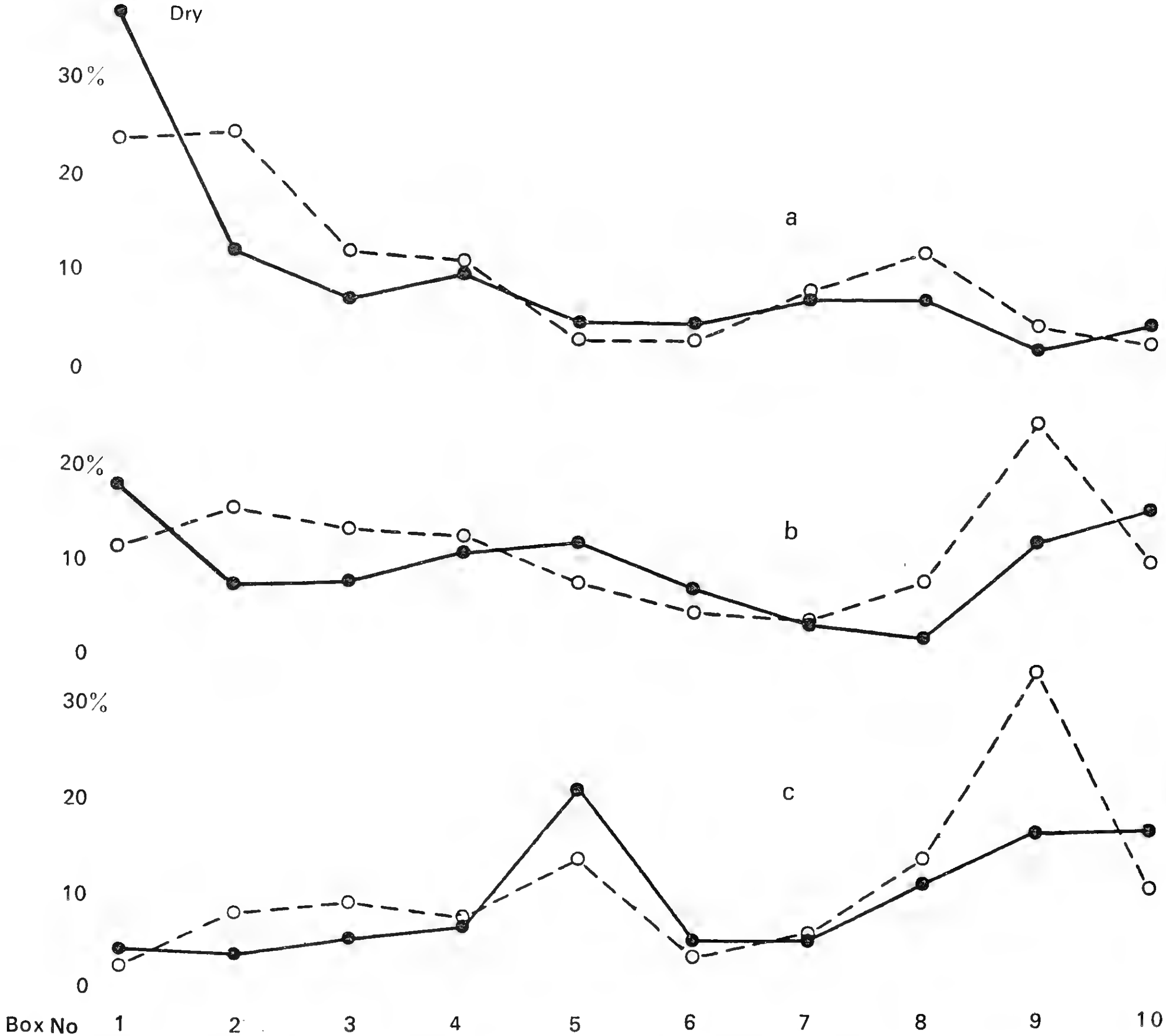


 Diagram 16. *Harpalus punctatulus*. Distribution according to humidity in the universal gradient apparatus in different months. Cf. Diagram 8. Continuous line—Empirical curve; Broken line—Curve obtained after correction according to curve in Diagram 15a. a—June 26, 40 specimens (Experiment $112b^1$, p. 99); b—July 10, July 12, 70 specimens (Experiment $112b^3$, p. 99); c—August 8, August 10, 71 specimens (Experiment $112b^2$, p. 99).

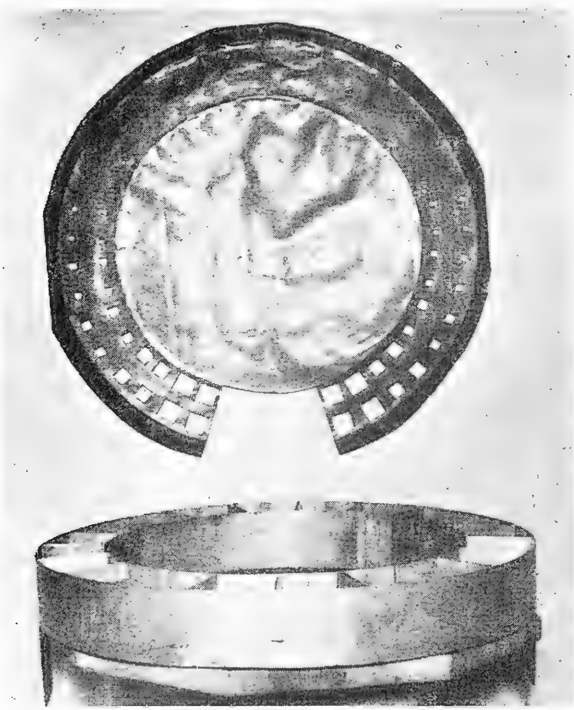
but satisfactory ecological and zoogeographical, answers can be derived, since they often show only a *ranking order* among a series of species. Finally, the experiments with the universal gradient apparatus actually highlighted certain points on the interaction of two factors (temperature and humidity), about which I was unable to obtain an explanation in any other way.

96 In the universal gradient apparatus only species of the genus *Harpalus* were studied. The entire experimental material used (with the exception of some specimens of *H. seladon*) originated from Öland and Gotland. It comprised old hibernated adults. It should therefore be as suitable for comparison as any.

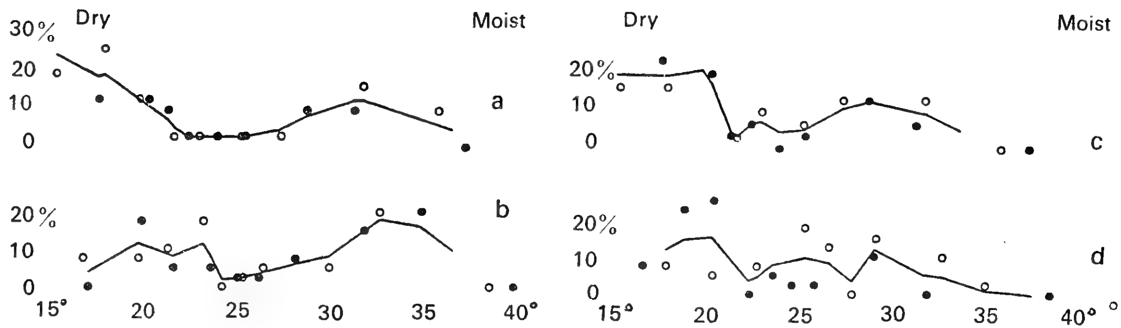
The results are all given coherently (p. 139 ff.); an indication with every experiment would therefore be superfluous.

The mean temperature calculated for each box in each experiment is evident from Diagrams 25–35 (p. 141 ff.).

With each of the 11 species treated the following 13 different experiments (always duplicated) were carried out:



94 Fig. 7. Circular universal gradient apparatus. Above: Black paper used in experiments with light factor.



95 Diagram 17. Duplicate 2-factor experiments (temperature, humidity) in linear (a, c) and in circular (b, d) universal gradient apparatus. Reduced clustering of insects in cold part of circular gradient apparatus. a and b—*Harpalus smaragdinus* (Experiment 117e, p. 102; Experiment 120d, p. 103 respectively); c and d—*H. rubripes* (Experiment 113e, p. 99; Experiment 120c, p. 103 respectively). See also explanation of diagrams for universal gradient apparatus, pp. 139 ff.

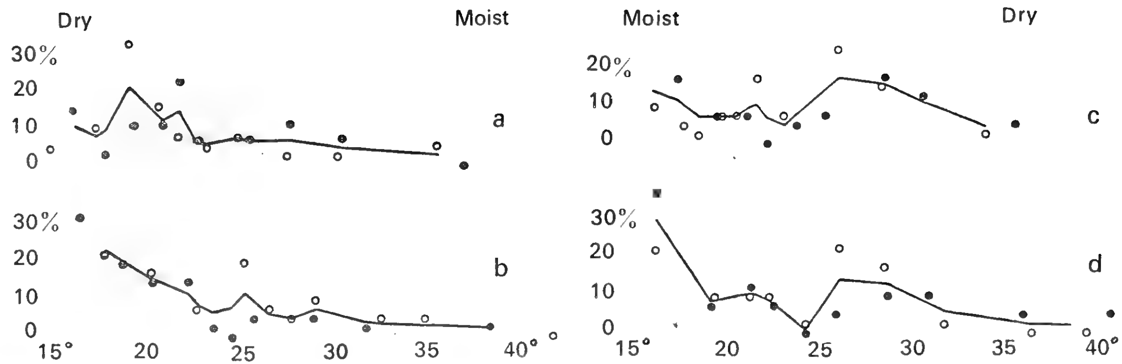


Diagram 18. Duplicate 2-factor experiments (temperature, humidity) in linear (a, c) and in circular (b, d) universal gradient apparatus. Clustering of insects at cold end of apparatus in all cases. a and b—*Harpalus melleti* (Experiment 111e, p. 98; Experiment 120a, p. 103 respectively). c and d—*H. punctatulus* (Experiment 112d, p. 99; Experiment 120b, p. 103 respectively). See also explanation of diagrams for universal gradient apparatus, pp. 139 ff.

a–c. Experiments with one factor (temperature, humidity, light), each taken separately.

d–i. Two-factor experiments.

d. Temperature + humidity ("warm-dry").

e. Temperature – humidity ("warm-moist").

f. Temperature + light ("warm-dark").

g. Temperature – light ("warm-light").

h. Humidity + light ("dry-dark").

i. Humidity – light ("dry-light").

j–m. Three-factor experiments.

j. Temperature + humidity + light ("warm-dry-dark").

k. Temperature + humidity – light ("warm-dry-light").

l. Temperature – humidity + light ("warm-moist-dark").

m. Temperature – humidity – light ("warm-moist-light").

Unless otherwise mentioned the *linear* universal gradient apparatus was used. The exposure always lasted 2 hours, at the most 10 minutes more or less.

Experiment 108. Harpalus aeneus. July 15–24, 1946. Öld Greby, June 11–15, 1946.

a^1. Temperature. July 18 through July 20, 2 experiments (with dry sawdust), total 60 specimens (together with *rubripes*).

a^2. July 20. 2 experiments (with slightly moist sawdust), total 60 specimens (together with *rubripes*).

b. Humidity. July 23. 2 experiments, total 60 specimens (together with *rubripes*).

c. Light. July 15, July 17. 2 experiments, total 60 specimens (together with *anxius*).

d. Temperature + humidity. July 17, July 18. 2 experiments, total 60 specimens (together with *rubripes*).

e. Temperature – humidity. July 15. 2 experiments, total 59 specimens (together with *anxius*).

f. Temperature + light. July 15, July 17. 2 experiments, total 60 specimens (together with *anxius*).

g. Temperature – light. July 20, July 21. 2 experiments, total 60 specimens (together with *rubripes*).

h. Humidity + light. July 20, July 23. 2 experiments, total 60 specimens (together with *rubripes*).

97 i. Humidity – light. July 24. 2 experiments, total 60 specimens (together with *rubripes*).

j. Temperature + humidity + light. July 17, July 18. 2 experiments, total 60 specimens (together with *rubripes*).

k. Temperature + humidity – light. July 21, July 23. 2 experiments, total 59 specimens (together with *rubripes*).

l. Temperature – humidity + light. July 15. 2 experiments, total 60 specimens (together with *anxius*).

m. Temperature – humidity – light. July 23. 2 experiments, total 60 specimens (together with *rubripes*).

Experiment 109. Harpalus anxius. July 14–25, 1946. Öld Stora-Rör, June 13, 1946.

a[1]. Temperature. July 24, July 25. 2 experiments (with dry sawdust), total 59 specimens (together with *smaragdinus* and *tardus*).

a[2]. July 22, July 24. 2 experiments (with slightly moist sawdust), total 60 specimens (together with *smaragdinus* and *tardus*).

b. Humidity. July 24, July 25. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

c. Light. July 15, July 17. 2 experiments, total 60 specimens (together with *aeneus*).

d. Temperature + humidity. July 14, July 19. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

e. Temperature – humidity. July 15. 2 experiments, total 59 specimens (together with *aeneus*).

f. Temperature + light. July 15, July 17. 2 experiments, total 60 specimens (together with *aeneus*).

g. Temperature – light. July 14. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

h. Humidity + light. July 19, July 22. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

i. Humidity – light. July 21, July 24. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

j. Temperature + humidity + light. July 14, July 19. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

k. Temperature + humidity – light. July 19, July 22. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

l. Temperature – humidity + light. July 15. 2 experiments, total 60 specimens (together with *aeneus*).

m. Temperature – humidity – light. July 21, July 22. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

Experiment 110. Harpalus azureus. July 3–10, 1946. Öld Greby, June 11–15, 1946.

a[1]. Temperature. July 3, July 7. 2 experiments, total 60 specimens (July 7, together with *rupicola*).

a[2]. July 25. 2 experiments (with slightly moist sawdust), total 60 specimens (together with *melleti* and *serripes*).

b. Humidity. July 8, July 10. 2 experiments, total 60 specimens (July 8, together with *rupicola*; July 10, together with *punctatulus*).

c. Light. July 8. 2 experiments, total 60 specimens (once together with *rupicola*).

d. Temperature + humidity. July 3, July 7. 2 experiments, total 60 specimens (July 7, together with *rupicola*).

e. Temperature – humidity. July 5. 2 experiments, total 59 specimens (once together with *rupicola*).

f. Temperature + light. July 3, July 6. 2 experiments, total 60 specimens (July 6, together with *rupicola*).

98 g. Temperature – light. July 5, July 6. 2 experiments, total 60 specimens (July 5, together with *rupicola*).

h. Humidity + light. July 9. 2 experiments, total 60 specimens (once together with *rupicola*).

i. Humidity – light. July 9, July 10. 3 experiments, total 90 specimens (twice together with *rupicola*).

j. Temperature + humidity + light. July 3, July 7. 2 experiments, total 60 specimens (July 7, together with *rupicola*).

k. Temperature + humidity – light. July 7. 2 experiments, total 60 specimens (once together with *rupicola*).

l. Temperature – humidity + light. July 5, July 6. 2 experiments, total 60 specimens (July 5, together with *rupicola*).

m. Temperature – humidity – light. July 5, July 6. 2 experiments, total 60 specimens (July 5, together with *rupicola*).

Experiment 111. Harpalus melleti. June 29 through August 9, 1945 (with the exception of $111a^2$). Gtl Visby, April 28–30, 1945 ($111a^2$, June 17, 1946).

a^1. Temperature. July 2–6, 1945. 3 experiments, total 114 specimens (once together with *punctatulus*, twice with *rupicola*, 3 times with *serripes*).

a^2. July 25, 1946. Gtl Visby, June 17, 1946. 2 experiments (with slightly moist sawdust), total 60 specimens (together with *azureus* and *serripes*).

b. Humidity. June 30, August 8, 1945. 2 experiments, total 65 specimens (once together with *punctatulus*, once with *rupicola*, twice together with *serripes*).

c. Light. June 29, August 8. 2 experiments, total 64 specimens (together with *serripes*, once also with *rupicola*).

d. Temperature + humidity. July 2, July 31. 2 experiments, total 66 specimens (together with *serripes*, once also with *punctatulus* and *rupicola*).

e. Temperature – humidity. July 5, August 2, 2 experiments, total 62 specimens (together with *serripes*, once with *rupicola*, once with *seladon*).

f. Temperature + light. July 3, July 31. 2 experiments, total 64 specimens (together with *serripes*, once with *rupicola*).

g. Temperature – light. July 5, July 31. 2 experiments, total 62 specimens (together with *serripes*, once each with *rupicola* and *seladon*).

h. Humidity + light. July 1, August 9. 2 experiments, total 65 specimens (together with *serripes*, once with *rupicola*).

i. Humidity – light. July 1, August 9. 2 experiments, total 64 specimens (together with *serripes*, once with *rupicola*).

j. Temperature + humidity + light. July 4, August 2. 2 experiments, total 63 specimens (together with *serripes*, once with *punctatulus* and *rupicola*, once with *seladon*).

k. Temperature + humidity – light. July 4, August 2. 2 experiments, total 63 specimens (together with *serripes*, once with *rupicola*).

l. Temperature – humidity + light. July 5, August 2. 2 experiments, total 62 specimens (together with *serripes*, once with *rupicola*).

m. Temperature – humidity – light. July 3, August 1. 2 experiments, total 63 specimens (together with *serripes*, once each with *rupicola* and *seladon*).

Experiment 112. Harpalus punctatulus. June 20 through August 10, 1945 (with the exception of 112a^2 and b^3). Gtl Visby, April 28, 1945. (112a^2; b^3, June 17, 1946).

a^1. Temperature. June 20 through July 2, 1945. 3 experiments, total 119 specimens (twice together with *seladon*, once with *melleti, rupicola, serripes*).

99 a^2. July 25, 1946. Gtl Visby, June 17, 1946. 2 experiments (with slightly moist sawdust), total 60 specimens (together with *rupicola* and *seladon*).

b^1. Humidity. June 26, 1945. 1 experiment, 40 specimens (together with *seladon*).

b^2. August 8, August 10, 1945. 3 experiments, total 71 specimens (once together with *seladon*, once with *melleti* and *serripes*).

b^3. July 10, July 12, 1946. Gtl Visby, June 17, 1946. 2 experiments, total 70 specimens (once together with *azureus*).

c. Light. June 21, August 8, 1945. 2 experiments, total 65 specimens (together with *seladon*).

d. Temperature + humidity. June 20, July 2. 2 experiments, total 80 specimens (once together with *seladon*, once with *melleti, rupicola, serripes*).

e. Temperature – humidity. June 27, June 30. 2 experiments, total 80 specimens (together with *seladon*).

f. Temperature + light. June 6, June 29. 2 experiments, total 80 specimens (together with *seladon*).

g. Temperature – light. June 27, July 5. 2 experiments, total 80 specimens (together with *seladon*).

h. Humidity + light. June 27, August 10. 2 experiments, total 64 specimens (together with *seladon*).

i. Humidity – light. June 28, August 11. 2 experiments, total 64 specimens (together with *seladon*).

j. Temperature + humidity + light. June 28, July 4. 2 experiments, total 80 specimens (once together with *seladon*, once with *melleti, rupicola, serripes*).

k. Temperature + humidity – light. June 28, August 1. 2 experiments, total 66 specimens (together with *seladon*).

l. Temperature – humidity + light. June 27, August 1. 2 experiments, total 66 specimens (together with *seladon*).

m. Temperature – humidity – light. June 28, June 30. 2 experiments, total 80 specimens (together with *seladon*).

Experiment 113. Harpalus rubripes. July 16–24, 1946. Öld Greby, June 11–15, 1946.

a^1. Temperature. July 18, July 20. 2 experiments, total 60 specimens (together with *aeneus*).

a^2. July 20. 2 experiments (with slightly moist sawdust), total 60 specimens (together with *aeneus*).

b. Humidity. July 23. 2 experiments, total 60 specimens (together with *aeneus*).

c. Light. July 16, July 18. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

d. Temperature + humidity. July 17, July 18. 2 experiments, total 60 specimens (together with *aeneus*).

e. Temperature – humidity. July 16. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

f. Temperature + light. July 16, July 18. 2 experiments, total 60 specimens (together with *smaragdinus* and *tardus*).

g. Temperature – light. July 20, July 21. 2 experiments, total 60 specimens (together with *aeneus*).

h. Humidity + light. July 20, July 23. 2 experiments, total 60 specimens (together with *aeneus*).

i. Humidity – light. July 24. 2 experiments, total 60 specimens (together with *aeneus*).

j. Temperature + humidity + light. July 17, July 18. 2 experiments, total 60 specimens (together with *aeneus*).

k. Temperature + humidity – light. July 21, July 23. 2 experiments, total 60 specimens (together with *aeneus*).

l. Temperature – humidity + light. July 16. 2 experiments, total 61 specimens (together with *smaragdinus* and *tardus*).

m. Temperature – humidity – light. July 23. 2 experiments, total 60 specimens (together with *aeneus*).

Experiment 114. Harpalus rupicola. June 29 through July 5, 1945 and July 5–25, 1946. Gtl Visby, April 28–30, 1945 and June 18, 1946, respectively.

100 a^1. Temperature. July 2, July 5, 1945. 2 experiments, total 39 specimens (together with *melleti* and *serripes,* once also with *punctatulus*).

a^2. July 25, 1946. 2 experiments (with slightly moist sawdust), total 59 specimens (together with *punctatulus* and *seladon*).

a^3. July 7, 1946. 1 experiment (with dry sawdust), 29 specimens (together with *azureus*).

b^1. Humidity. June 30, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

b^2. July 8, 1946. 1 experiment, 30 specimens (together with *azureus*).

c^1. Light. June 29, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

c^2. July 8, 1946. 1 experiment, 30 specimens (together with *azureus*).

d^1. Temperature + humidity. July 2, 1945. 1 experiment, 20 specimens (together with *melleti, punctatulus, serripes*).

d^2. July 7, 1946. 1 experiment, 30 specimens (together with *azureus*).

e^1. Temperature – humidity. July 3, July 5, 1945. 2 experiments, total 40 specimens (once with *melleti* and *serripes*).

e^2. July 5, 1946. 1 experiment, 29 specimens (together with *azureus*).

f^1. Temperature + light. July 3, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

f^2. July 6, 1946. 1 experiment, 30 specimens (together with *azureus*).

g^1. Temperature – light. July 5, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

g^2. July 5, 1946. 1 experiment, 29 specimens (together with *azureus*).

h^1. Humidity + light. July 1, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

h^2. July 9, 1946. 1 experiment, 30 specimens (together with *azureus*).

i^1. Humidity – light. July 1, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

i^2. July 10, 1946. 1 experiment, 30 specimens (together with *azureus*).

j^1. Temperature + humidity + light. July 4, 1945. 1 experiment, 20 specimens (together with *melleti, punctatulus* and *serripes*).

j^2. July 7, 1946. 1 experiment, 30 specimens (together with *azureus*).

k^1. Temperature + humidity – light. July 4, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

k^2. July 7, 1946. 1 experiment, 30 specimens (together with *azureus*).

l^1. Temperature – humidity + light. July 5, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

l^2. July 5, 1946. 1 experiment, 30 specimens (together with *azureus*).

m^1. Temperature – humidity – light. July 3, 1945. 1 experiment, 20 specimens (together with *melleti* and *serripes*).

m^2. July 5, 1946. 1 experiment, 30 specimens (together with *azureus*).

Experiment 115. Harpalus seladon. June 20 through July 5, 1945; Gtl Visby, April 30, 1945. July 31 through August 11, 1945; Upl. Värmdön, Västerskägga, July 1945. July 25, 1946; Öld Greby, June 11–15, 1946.

a^1. Temperature. June 20, June 28, June 29, August 1, 1945. 4 experiments, total 129 specimens (three times with *punctatulus,* once with *serripes*).

a^2. July 25, 1946. 2 experiments (with slightly moist sawdust), total 59 specimens (together with *punctatulus* and *rupicola*).

b. Humidity. June 26, August 8, 1945. 2 experiments, total 59 specimens (together with *punctatulus*).

c. Light. June 21, August 8, 1945. 2 experiments, total 66 specimens (together with *punctatulus*).

d. Temperature + humidity. June 20, August 1, 1945. 2 experiments, total 72 specimens (once together with *punctatulus,* once with *serripes*).

e. Temperature – humidity. June 27, June 30, August 2, 1945. 3 experiments, total 92 specimens (twice with *punctatulus,* once with *melleti* and *serripes*).

101 f. Temperature + light. June 29, August 3, 1945. 2 experiments, total 62 specimens (together with *punctatulus*).

g. Temperature – light. June 27, July 5, July 31, 1945. 3 experiments, total 92 specimens (twice with *punctatulus,* once along with *melleti* and *serripes*).

h. Humidity + light. June 27, August 10, 1945. 2 experiments, total 65 specimens (together with *punctatulus*).

i. Humidity – light. June 28, August 11, 1945. 2 experiments, total 62 specimens (together with *punctatulus*).

j. Temperature + humidity + light. June 28, August 2, 1945. 2 experiments, total 67 specimens (once along with *punctatulus,* once with *melleti* and *serripes*).

k. Temperature + humidity – light. June 28, August 1, 1945. 2 experiments, total 65 specimens (together with *punctatulus*).

1. Temperature – humidity + light. June 27, August 1, 1945. 2 experiments, total 66 specimens (together with *punctatulus*).

m. Temperature – humidity – light. June 28, June 30, 1945. 2 experiments, total 54 specimens (together with *punctatulus*).

Experiment 116. Harpalus serripes. June 29, through August 9, 1945 (except $116a^2$). Gtl Visby, April 29, 1945 (except $116a^2$).

a^1. Temperature. July 2, 3, 5, August 1, 1945. 4 experiments, total 83 specimens (three times together with *melleti*, twice with *rupicola,* once each with *punctatulus* and *seladon*).

a^2. July 25, 1946. Öld Greby, June 11–15, 1946. 2 experiments (with slightly moist sawdust), total 60 specimens (together with *azureus* and *melleti*).

b. Humidity. June 30, August 8, 1945. 2 experiments, total 42 specimens (together with *melleti,* once each with *punctatulus* and *rupicola*).

c. Light. June 29, August 8. 2 experiments, total 42 specimens (together with *melleti,* once with *rupicola*).

d. Temperature + humidity. July 2, 31, August 1. 3 experiments, total 63 specimens (twice along with *melleti,* once each with *punctatulus, rupicola, seladon*).

e. Temperature – humidity. July 5, August 2. 2 experiments, total 43 specimens (together with *melleti,* once each with *rupicola* and *seladon*).

f. Temperature + light. July 5, 31. 2 experiments, total 43 specimens (together with *melleti*, once each with *rupicola* and *seladon*).

g. Temperature – light. July 5, 31. 2 experiments, total 43 specimens (together with *melleti*, once each with *rupicola* and *seladon*).

h. Humidity + light. July 1, August 9. 2 experiments, total 42 specimens (together with *melleti*, once with *rupicola*).

i. Humidity – light. July 1, August 9. 2 experiments, total 42 specimens (along with *melleti*, once with *rupicola*).

j. Temperature + humidity + light. July 4, August 2. 2 experiments, total 43 specimens (along with *melleti*, once each with *rupicola* and *seladon*).

k. Temperature + humidity – light. July 4, August 2. 2 experiments, total 42 specimens (together with *melleti*, once with *rupicola*).

l. Temperature – humidity + light. July 5, August 2. 2 experiments, total 43 specimens (together with *melleti*, once with *rupicola*).

m. Temperature – humidity – light. July 3, August 1. 2 experiments, total 43 specimens (together with *melleti*, once each with *rupicola* and *seladon*).

Experiment 117. Harpalus smaragdinus. July 14–25, 1946. Öld Stora-Rör, June 13, 1946.

a^1. Temperature. July 24, 25. 2 experiments, total 61 specimens (together with *anxius* and *tardus*).

102 a^2. July 22, 24. 2 experiments (with slightly moist sawdust), total 60 specimens (together with *anxius* and *tardus*).

b. Humidity. July 24, 25. 2 experiments, total 60 specimens (together with *anxius* and *tardus*).

c. Light. July 16, 18. 2 experiments, total 60 specimens (together with *rubripes* and *tardus*).

d. Temperature + humidity. July 14, 19. 2 experiments, total 60 specimens (together with *anxius* and *tardus*).

e. Temperature – humidity. July 16. 2 experiments, total 60 specimens (together with *rubripes* and *tardus*).

f. Temperature + light. July 16, 18. 2 experiments, total 60 specimens (together with *rubripes* and *tardus*).

g. Temperature – light. July 14. 2 experiments, total 60 specimens (together with *anxius* and *tardus*).

h. Humidity + light. July 19, 22. 2 experiments, total 60 specimens (together with *anxius* and *tardus*).

i. Humidity – light. July 21, 24. 2 experiments, total 60 specimens (together with *anxius* and *tardus*).

j. Temperature + humidity + light. July 14, 19. 2 experiments, total 60 specimens (together with *anxius* and *tardus*).

k. Temperature + humidity – light. July 19, 22. 2 experiments, total 60 specimens (together with *anxius* and *tardus*).

l. Temperature – humidity + light. July 16. 2 experiments, total 60 specimens (together with *rubripes* and *tardus*).

m. Temperature – humidity – light. July 21, 22. 2 experiments, total 60 specimens (together with *anxius* and *tardus*).

Experiment 118. Harpalus tardus. July 14–25, 1946. Öld and Gtl June 14–18, 1946.

a[1]. Temperature. July 24, 25. 2 experiments, total 48 specimens (together with *anxius* and *smaragdinus*).

a[2]. July 22, 24. 2 experiments (with slightly moist sawdust), total 49 specimens (together with *anxius* and *smaragdinus*).

b. Humidity. July 24, 25. 2 experiments, total 48 specimens (together with *anxius* and *smaragdinus*).

c. Light. July 16, 18. 2 experiments, total 54 specimens (together with *rubripes* and *smaragdinus*).

d. Temperature + humidity. July 14, 19. 2 experiments, total 54 specimens (together with *anxius* and *smaragdinus*).

e. Temperature – humidity. July 16. 2 experiments, total 54 specimens (together with *rubripes* and *smaragdinus*).

f. Temperature + light. July 16, 18. 2 experiments, total 54 specimens (together with *rubripes* and *smaragdinus*).

g. Temperature – light. July 14. 2 experiments, total 54 specimens (together with *anxius* and *smaragdinus*).

h. Humidity + light. July 19, 22. 2 experiments, total 51 specimens (together with *anxius* and *smaragdinus*).

i. Humidity – light. July 21, 24. 2 experiments, total 50 specimens (together with *anxius* and *smaragdinus*).

j. Temperature + humidity + light. July 14, 19. 2 experiments, total 53 specimens (together with *anxius* and *smaragdinus*).

k. Temperature + humidity – light. July 19, 22; 2 experiments, total 51 specimens (together with *anxius* and *smaragdinus*).

103 l. Temperature – humidity + light. July 16. 2 experiments, total 54 specimens (together with *rubripes* and *smaragdinus*).

m. Temperature – humidity – light. July 21, 22. 2 experiments, total 50 specimens (together with *anxius* and *smaragdinus*).

Distribution in the linear universal gradient apparatus without the influence of measurable factors (control experiment)

Experiment 119. Harpalus melleti, punctatulus, seladon and *serripes*. August 11–13, 1945. Gtl Visby, April 28–30, 1945; except *seladon,* which was collected in July 1945 near Upl Värmdön, Västerskägga. Exposure 2 hours, 2 species tested every time with 20 specimens of each. All species tested 5 times, thus total 100 specimens per species. Dry sawdust in the boxes. Diagram 15, p. 91.

Control experiments in the circular universal gradient apparatus
Only experiments covered in the text are mentioned here (Diagrams 17, 18, p. 95).

Experiment 120. July 10–11, 1946.

a. *Harpalus melleti.* Temperature – humidity. Gtl Visby, June 17, 1946. 2 experiments, July 10–11, total 80 specimens.

b. *Harpalus punctatulus.* Temperature + humidity. Gtl Visby, June 17, 1946. 2 experiments, July 11, total 80 specimens.

c. *Harpalus rubripes.* Temperature – humidity. Öld Greby, June 11–15, 1946. 2 experiments, July 10–11, total 80 specimens.

d. *Harpalus smaragdinus.* Temperature – humidity. Öld Stora-Rör, June 13, 1946. 2 experiments, July 10, total 80 specimens.

IV. Food Preference

Only one species, *Amara ingenua*, was experimentally studied in this connection. One animal was placed in each glass dish with moist filter paper, where it was simultaneously provided with different seeds and fruits, in one case also animal food. The signs of feeding were recorded every morning.

Experiment 121. September 5–9, 1946. Upl Solna, Bergshamra, August 30, 1946. 8 specimens isolated from one another in glass dishes and provided with seeds and fruits of 13 different species of plants. Table 33, p. 539.

Experiment 122. September 18–19, 1946. The same 8 specimens. Each one of which was provided with 3 fruits of *Polygonum aviculare* and in addition 3 young pods each of *Capsella* and *Erysimum cheiranthoides*; p. 539.

Experiment 123. September 21–22, 1946. 4 of the above specimens were each provided with 3 fruits of *Polygonum aviculare* and in addition a crushed insect of their own species; p. 540.

104 B. EXPERIMENTS ON RESISTANCE

I. Low Temperatures

The animals were cooled in a cooling chamber until complete cessation of all movement, and then (by disconnecting the electricity) very slowly warmed up (about 1°C in 10 minutes). All animals were initially placed on their backs and the temperature was noted when each individual reverted to its normal position. In several cases the temperature at which the first signs of life were noticed was also recorded. Observation was carried out through the front window of the refrigerator. The thermometer was placed in the glass dish (the bottom was covered with filter paper) containing the animals.

These experiments were carried out following Krogerus' model (1932, pp. 145–146; 1937; p. 306). However, I have not taken into account his third

response point ("full activity of the experimental animals") because I found it impossible to determine this exactly. Besides, "Point 1," initial movement, is rather vague, especially in the case of small species, since this often involves the slightest quivering of the palps or tarsi. Due to uneven refraction through the glass panel the slightest movement of the observer's head can give the impression of such a micromovement. It also happened that an animal that had been lying apparently lifeless suddenly turned over and immediately showed full activity. The "point of turnover" is undoubtedly the most important, for it is an expression of the lower thermic level of activity of the animal.

The two most important sources of error in these experiments are:

1. The animals frequently show different individual responses (more with respect to "the first movement" than to the "point of turnover"). The cooling occasionally causes death; in other cases there is a distinct shock effect (paralysis of the extremities).

2. The velocity of and the amount of cooling, which, on the one hand, depend on the starting temperature and, on the other hand, the reduction necessary to reach the condition of immobility, the cooling time may cause different intensities of paralysis in the animals.

It is clear that in these experiments, it is as impossible to obtain *absolute* values for each species as with the temperature gradient apparatus. The "point of turnover" after a brief cooling (as in these experiments) probably lies below the actual temperature of the lower limit of activity at the time of waking up of the animal in spring.

It is therefore once again advisable to seek only *comparative values*, i.e.,
105 the experiments must always proceed simultaneously (or at any rate as far as possible under identical conditions) with 2 or more species for the purpose of comparison. That the values obtained with extensive material at least do not seem to coincide too much has been shown by their identity in the case of *Brachynus* versus *Agonum dorsale* (p. 61).

All the experiments were carried out in the "Statens Växtskyddanstalt" (State Institute of Plant Protection), Stockholm.

Harpalus, see Diagram 20 (p. 130); *Cymindis,* see p. 139.

Experiment 124. June 27, 1946. Room temperature 21.1°C.

a. *Agonum dorsale*. Öld Greby, June 11–15, 1946. 2 specimens; p. 61.

b. *Amara lucida*. Öld Greby, June 11–15, 1946. 3 specimens (+ 3.5, 5.4, 6.0 and 7.6, 7.6, 7.8°C respectively)*.

c. *Brachynus crepitans*. Upl Lovön, May 1946. 2 specimens; p. 61.

d. *Calathus melanocephalus*. Öld Greby, June 11–15, 1946. 3 specimens (−1.3, +1.0, 1.0 and 4.9, 5.6, 5.7°C respectively)*.

e. *Calathus mollis*. Öld Greby, June 11–15, 1946. 3 specimens (+ 1.2, 3.9, 6.0 and 6.2, 7.1, 7.7°C respectively)*.

*Not treated in the text.

Experiment 125. June 28, 1946. Room temperature 20.4–20.8°C.
a. *Cymindis angularis*. Öld Greby, June 11–15, 1946. 3 specimens.
b. *Cymindis humeralis*. Öld Greby, June 11–15, 1946. 2 specimens.
c. *Cymindis macularis*. Öld Stora-Rör, June 13, 1946. 3 specimens.
d. *Harpalus aeneus*. Öld Greby, June 11–15, 1946. 3 specimens.
e. *Harpalus azureus*. Öld Greby, June 11–15, 1946. 3 specimens.
f. *Harpalus melleti*. Gtl Visby, June 19, 1946. 3 specimens.
g. *Harpalus punctatulus*. Gtl Visby, June 18, 1946. 3 specimens.
h. *Harpalus puncticeps*. Öld Halltorp, June 16, 1946. 2 specimens.
i. *Harpalus rupicola*. Gtl Visby, June 18, 1946. 3 specimens.
j. *Harpalus seladon*. Öld Greby, June 11–15, 1946. 3 specimens.
Experiment 126. June 29, 1946. Room temperature 20.1–20.3°C.
a. *Harpalus hirtipes*. Öld Stora-Rör, June 13, 1946. 3 specimens.
b. *Harpalus neglectus*. Öld Stora-Rör, June 13, 1946. 3 specimens.
c. *Harpalus rubripes*. Öld Greby, June 11–15, 1946. 1 specimen.
d. *Harpalus rufitarsis*. Öld Stora-Rör, June 13, 1946. 3 specimens.
e. *Harpalus tardus*. Öld and Gtl, June 11–18, 1946. 3 specimens.
f. *Harpalus vernalis*. Öld Stora-Rör, June 13, 1946. 3 specimens (+0.9, 3.6, 3.8 and 6.9, 7.0, 7.6°C respectively)*.
Experiment 127. July 1, 1946. Room temperature about 21°C.
a. *Cymindis humeralis*. Öld Greby, June 11–15, 1946. 1 specimen.
b. *Cymindis macularis*. Öld Stora-Rör, June 3, 1946. 1 specimen.
c. *Harpalus aeneus*. Öld Greby, June 11–15, 1946. 2 specimens.
d. *Harpalus anxius*. Öld Stora-Rör, June 13, 1946. 3 specimens.
e. *Harpalus rubripes*. Öld Greby, June 11–15, 1946. 3 specimens.
f. *Harpalus serripes*. Öld Greby, June 11–15, 1946. 3 specimens.
g. *Harpalus smaragdinus*. Öld Stora-Rör, June 13, 1946. 3 specimens.
106 *Experiment 128*. June 26, 1947. Öld Greby, June 12–22, 1947. Room temperature about 23°C.
a. *Agonum dorsale*. 10 ♂, 10 ♀ (recorded separately); p. 61.
b. *Brachynus crepitans*. 10 ♂, 10 ♀ (recorded separately); p. 61.
c. *Calathus mollis*, macropterous form. 5 ♂, 5 ♀ (recorded separately); p. 358.
d. *Calathus mollis*, brachypterous form. 5 ♂, 5 ♀ (recorded separately); p. 358.
e. *Harpalus azureus*. 5 ♂, 5 ♀ (recorded separately); p. 191.
Experiment 129. June 28, 1947. Öld Greby, June 12–22, 1947. Room temperature about 23°C.
a. *Agonum dorsale*. 10 ♂, 10 ♀ (recorded separately); p. 61.
b. *Brachynus crepitans*. 10 ♂, 10 ♀ (recorded separately); p. 61.
c. *Harpalus azureus*. 5 ♂, 5 ♀ (recorded separately); p. 191.

*Not treated in the text.

Experiment 130. September 19, 1947. Room temperature 23°C.

a. *Bradycellus collaris,* macropterous form. 20 specimens. Jtl Revsund, August 31, 1947. p. 359.

b. *Bradycellus collaris,* brachypterous form. 20 specimens. Jtl Revsund, August 31, 1947. p. 359.

c. *Lionychus quadrillum.* 3 specimens. Nke Örebro, August 20, 1947. "Point of turnover": – 1.8, + 2.3, 3.2°C.

II. High Temperatures

The animals were placed in a tin box whose bottom was covered with filter paper and the top with a glass lid. A thermometer was placed at the bottom. The box was slowly warmed up (about 1°C in 2 minutes) in a water bath, and for each individual the temperatures of the first sign of paralysis and the last body movement (Points 4 and 5, Krogerus, 1932, p. 146; 1937, p. 306) were recorded.

The individual variations in the above-mentioned temperatures were generally not large. The chief external sources of error might be the initial temperature and the humidity of the air. However, all the experiments were carried out in the same room in July at a temperature of 23.8–26.2°C. In the relative humidity of the air greater variation than 60 to 70% could not have occurred.

Concerning the species of *Harpalus*, see Diagram 20 (p. 130); *Cymindis*, p. 139.

Experiment 131. July 24, 1946. Room temperature about 26°C. The figures obtained are not treated in the text.

a. *Amara equestris.* Öld Greby, June 11–15, 1946. 2 specimens (43.8, 43.8 and 45.7, 46.1°C respectively).

b. *Calathus mollis.* Öld Greby, June 11–15, 1946. 3 specimens (36.3, 38.8, 40.3 and 42.7, 43.6, 43.7°C respectively).

c. *Panagaeus bipustulatus.* Öld Greby, June 11–15, 1946. 3 specimens (46.3, 46.3, 46.9 and 47.6, 47.6, 48.6°C, respectively).

Experiment 132. July 27, 1946. Room temperature 25.5–25.9°C.

a. *Harpalus azureus.* Öld Greby, June 11–15, 1946. 3 specimens.

b. *Harpalus melleti.* Gtl Visby, June 19, 1946. 3 specimens.

c. *Harpalus punctatulus.* Gtl Visby, June 19, 1946. 3 specimens.

d. *Harpalus rupicola.* Gtl Visby, June 19, 1946. 3 specimens.

107 e. *Harpalus seladon.* Gtl Visby, June 19, 1946. 3 specimens.

f. *Harpalus serripes.* Öld Greby, June 11–15, 1946. 3 specimens.

Experiment 133. July 28, 1946. Room temperature 25.6–26.2°C.

a. *Harpalus aeneus.* Öld Greby, June 11–15, 1946. 3 specimens.

b. *Harpalus anxius.* Öld Stora-Rör, June 13, 1946. 3 specimens.

c. *Harpalus puncticeps*. Öld Halltorp, June 16, 1946. 3 specimens.

d. *Harpalus vernalis*. Öld Greby, June 11–15, 1946. (48.1, 48.7, 48.8 and 49.1, 49.2, 49.3°C respectively)*.

Experiment 134. July 28, 1946. Room temperature 23.8°C.

a. *Cymindis angularis*. Öld Greby, June 11–15, 1946. 3 specimens.

b. *Cymindis humeralis*. Öld Greby, June 11–15, 1946. 3 specimens.

Experiment 135. July 29, 1946. Room temperature 23.9°C.

a. *Harpalus hirtipes*. Öld Stora-Rör, June 13, 1946. 3 specimens.

b. *Harpalus rubripes*. Öld Greby, June 11–15, 1946. 3 specimens.

Experiment 136. July 30, 1946. Room temperature 24.6–24.9°C.

a. *Amara lucida*. Öld Greby, June 11–15, 1946. 3 specimens (46.4, 46.7, 47.6 and 47.6, 48.3, 48.6°C respectively)*.

b. *Cymindis macularis*. Öld Stora-Rör, June 13, 1946. 3 specimens.

c. *Harpalus aeneus*. Öld Greby, June 11–15, 1946. 3 specimens.

d. *Harpalus azureus*. Öld Greby, June 11–15, 1946. 3 specimens.

e. *Harpalus hirtipes*. Öld Stora-Rör, June 13, 1946. 3 specimens.

f. *Harpalus neglectus*. Öld Stora-Rör, June 13, 1946. 3 specimens.

g. *Harpalus rufitarsis*. Öld Stora-Rör, June 13, 1946. 3 specimens.

h. *Harpalus smaragdinus*. Öld Stora-Rör, June 13, 1946. 3 specimens.

i. *Harpalus tardus*. Öld and Gtl, June 11–19, 1946. 3 specimens.

Experiment 137. July 10–11, 1947. Room temperature 26°C. Öld Greby, June 12–23, 1947; p. 61.

a. *Agonum dorsale*. 10 ♂ (2 experiments).

b. *Agonum dorsale*. 10 ♀ (2 experiments).

c. *Brachynus crepitans*. 10 ♂ (2 experiments).

d. *Brachynus crepitans*. 10 ♀ (2 experiments).

III. Drought

The animals were placed, each species separately (occasionally form or sex as well), in a small completely dry glass dish with filter paper at the bottom, and the maximum life-span of each individual without water and food was recorded. Observations were recorded every 4 to 9 hours.

An important source of error is undoubtedly the humidity of the air. However, since the experiments were carried out in the room during the period from June 26 through August 22, the values obtained might be comparable. Experiment 142 (September 23 through October 1) was an exception; but the
108 purpose here was to exclusively compare the 2 forms of this species.

Experiment 138. From July 25, 1946 onward. Diagram 23, p. 135 (with the exception of *Amara, Cymindis*, and *Harpalus vernalis*).

*Not treated in the text.

a. *Amara lucida*. Öld Greby, June 11–15, 1946. 3 specimens (58, 91, and 106 hours respectively)*.

b. *Cymindis angularis*. Öld Greby, June 11–15, 1946. 3 specimens; p. 139.

c. *Cymindis humeralis*. Öld Greby, June 11–15, 1946. 3 specimens; p. 139.

d. *Harpalus aeneus*. Öld Greby, June 11–15, 1946. 3 specimens.

e. *Harpalus anxius*. Öld Stora-Rör, June 13, 1946. 3 specimens.

f. *Harpalus azureus*. Öld Greby, June 11–15, 1946. 3 specimens.

g. *Harpalus melleti*. Gtl Visby, June 19, 1946. 3 specimens.

h. *Harpalus punctatulus*. Gtl Visby, June 19, 1946. 3 specimens.

i. *Harpalus puncticeps*. Öld Halltorp, June 16, 1946. 3 specimens.

j. *Harpalus rubripes*. Öld Greby, June 11–15, 1946, 3 specimens.

k. *Harpalus rupicola*. Gtl Visby, June 19, 1946. 3 specimens.

l. *Harpalus seladon*. Gtl Visby, June 19, 1946. 3 specimens.

m. *Harpalus serripes*. Öld Greby, June 11–15, 1946. 3 specimens.

n. *Harpalus vernalis*. Öld Greby, June 11–15, 1946. 3 specimens (45, 58 and 125 hours respectively)*.

Experiment 139. From August 1, 1946 onward. Diagram 23, p. 135 (without *Cymindis*).

a. *Cymindis macularis*. Öld Stora-Rör, June 13, 1946. 3 specimens; p. 139.

b. *Harpalus hirtipes*. Öld Stora-Rör, June 13, 1946. 3 specimens.

c. *Harpalus neglectus*. Öld Stora-Rör, June 13, 1946. 3 specimens.

d. *Harpalus rufitarsis*. Öld Stora-Rör, June 13, 1946. 3 specimens.

e. *Harpalus smaragdinus*. Öld Stora-Rör, June 13, 1946. 3 specimens.

f. *Harpalus tardus*. Öld and Gtl, June 11–19, 1946. 3 specimens.

Experiment 140. From June 26, 1947 onward.

Calathus mollis. Öld Greby, June 12–22, 1947, p. 359.

a. Macropterous form. 4 ♂, 4 ♀ (recorded separately).

b. Brachypterous form. 4 ♂, 4 ♀ (recorded separately).

Experiment 141. From July 10, 1947 onward. Öld Greby, June 12–22, 1947; p. 61.

a. *Agonum dorsale*. 5 ♂ + 5 ♀, 5 ♂ + 5 ♀ (2 experiments).

b. *Brachynus crepitans*. 5 ♂ + 5 ♀, 5 ♂ + 5 ♀ (2 experiments).

Experiment 142. From September 23, 1947 onward. *Bradycellus collaris*. Jtl Revsund, August 31, 1947, p. 359.

a. Macropterous form, 10 specimens.

b. Brachypterous form, 10 specimens.

IV. Water

The few experiments on exposure to water were carried out in small vertical test tubes which were filled up to two-thirds with spring water. In each tube

*Not treated in the text.

there was always one animal. Each time two series of experiments were undertaken: in one the animals were allowed to swim undisturbed on the surface, in
109 the other the test tube was inverted three times a day in order to simulate to some extent the natural conditions during transport in water. The temperature of the air in the room was high (20–25°C), and therefore the values obtained on the duration of life are undoubtedly lower than in similar situations in nature. *Cymindis*, see p. 248.

Experiment 143. Cymindis angularis. From June 25, 1947 onward. Öld Greby, June 12–23, 1947.

a. 3 specimens. Left undisturbed.
b. 3 specimens. Regularly shaken.

Experiment 144. Cymindis humeralis. From June 25, 1947 onward. Öld Greby, June 12–23, 1947.

a. 3 specimens. Left undisturbed.
b. 3 specimens. Regularly shaken.

Experiment 145. Cymindis macularis. From June 25, 1947 onward. Öld Stora-Rör, June 14, 1947.

a. 3 specimens. Left undisturbed.
b. 3 specimens. Regularly shaken.

Experiment 146. Broscus cephalotes. From August 16, 1947 onward. Nl Tvärminne, August 12, 1947, p. 599.

a. 2 specimens. Left undisturbed.
b. 2 specimens. Regularly shaken.

C. EXPERIMENTS ON THE DIRECTION OF FLIGHT

A special apparatus was constructed whose appearance and dimensions are shown in Fig. 8 (see also Lindroth, 1948d). The lower part shown in the Figure was covered with a tight-fitting 45 cm high bell jar covered with cellophane.

The principle involved is that beetles flying out from a glass dish in the center of the apparatus would collide with the transparent walls of the bell
110 and fall into the corresponding funnels, whose spouts were directed into a glass jar.

It was intended to study the influence of the position of the sun on the flight of the insects. Therefore all the experiments were carried out around 6 p.m. (5–7 p.m.) and one of the sectors was directed towards the sun, i.e. westward. Due to the distribution of the animals in different sectors the direction of flight was recorded by constructing "flight paths" ("Flugrosen") (Fig. 21, p. 255). See also Table 19 (p. 257).

Experiment 147. Acupalpus consputus. Öld Halltorp, June 13–15, 1947 (about 60 specimens). All experiments carried out near Öld Greby, June 19–23, 5:30–7:00 p.m., total 200 observations.

Experiment 148. Acupalpus dorsalis.

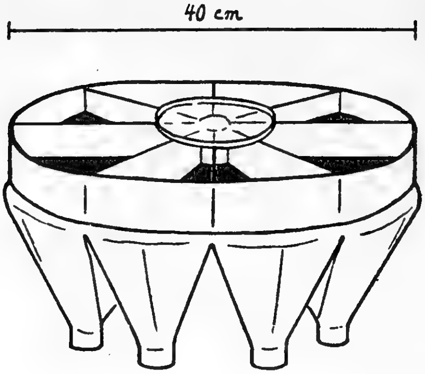


Fig. 8. Lower part of the flight direction apparatus. Experiment 147 onward.

a. Öld Möckelmossen, June 18, 1947 (8 specimens). Experiments near Öld Greby, June 19–23, 1947. 5:30–7:00 p.m., total 14 observations.

b. Nl Tvärminne, August 10–11, 1947 (about 70 specimens). Experiment in Djursholm, August 14, 5:15–6:00 p.m. (sunny, followed by overcast sky), total 77 observations.

Experiment 149. Badister dilatatus. Öld Halltorp, June 13–15, 1947 (about 30 specimens). Experiments carried out in Öld Greby, June 19–23, 5:30–7:00 p.m., total 34 observations.

Experiment 150. Badister peltatus. Öld Halltorp, June 13–15, 1947 (12 specimens). Experiments carried out in Öld Greby, June 19–23, 5:30–7:00 p.m., total 15 observations.

Experiment 151. Badister unipustulatus. Öld Halltorp, June 13–15, 1947 (15 specimens). Experiments conducted in Öld Greby, June 19–23, 5:30–7:00 p.m., total 27 observations.

Experiment 152. Oodes gracilis. Upl Djursholm, Ösby Lake, May 31, 1947 (about 50 specimens). The experiments were carried out in Djursholm, June 8, Gtl Visby, June 10, Öld Greby, June 12–18, 6:00–6:30 p.m., total 100 observations. Fig. 21.

D. EXPERIMENTS WITHOUT INSECTS

All these experiments are related to the studies on "limestone species" (pp. 112 ff.). They were carried out with the purpose of comparing the characteristics of the limestone rock and the basement complex (besides the loose deposits originating from these). Since these experiments are discussed in detail in the running text only brief notes are given here. Unless otherwise mentioned

these experiments were carried out in Djursholm.

Experiment 153. Daily temperature conditions on underside of pieces of limestone and granite. Diagram 36, p. 179. Studies carried out on the roof of the Institute in Djursholm from July 1, 1945, 5 a.m., through July 2, 1945, 6 a.m. Detailed account on p. 178.

Experiment 154. Daily temperature conditions in small volumes of limestone gravel and siliceous gravel. Diagram 37, p. 180. Simultaneously realized with Experiment 153. Description of gravel as on p. 77. Temperature recorded in 4
111 samples, each in a 400 cm^3 zinc box, to which 100, 50, 25, and 0 cm^3 of water was added respectively. Description on p. 178.

Experiment 155. Temperature conditions in limestone and siliceous gravels over longer period of time. September 4 through October 29, 1945. Same boxes and categories of gravel as in Experiment 154. But a minimum thermometer was used, inserted horizontally through the walls of the boxes. The boxes were placed in the open but protected from rain by an overhanging roof. The minimum temperature was read every day and usually also at 11 a.m., 4 p.m., and 9 p.m.; p. 178.

Experiment 156. Temperature conditions in limestone and siliceous gravels with heating. The same methods as in Experiment 155.

a. February 10, 1946. The boxes remained in the open for several months. On February 10, with an outside temperature of −10.7°C, they were abruptly brought into a room at a temperature of +17.6°C and the temperature of the gravel was recorded regularly (every minute during the first hour-and-a-quarter). The gravel was apparently completely dried and hence considerable condensation of water must have taken place. Diagram 38, p. 182.

b. March 3, 1947. Repetition of a). Outside temperature −9.3°C, room temperature +18.2°C. The boxes were cooled only for one day prior to the experiment and the gravel was apparently not quite dry. The curves did not intersect. p. 181.

c. March 7, 1947. Outside temperature −11.0°C, room temperature +17.1–17.4°C. Repeated as in b) with the same result. p. 181.

Experiment 157. Temperature conditions in limestone and siliceous gravels during strong cooling. March 14–15, 1946. Opposite to Experiment 156. The boxes were kept inside the room from February 10 through March 14. Starting temperature +18.1°C. Outside temperature −6.1 to −16.1°C (at the end of the experiment at 1:35 a.m.). Since the air temperature fell constantly during the experiment (minimum night temperature: −19.0°C), the curves did not meet. Diagram 39, p. 182.

Experiment 158. Evaporation of water from limestone gravel and siliceous gravel. September 8 through October 3, 1946. The same boxes and categories of gravel as in Experiments 154–157. To the volumes of limestone and siliceous gravel (400 cm^3 each) 100 cm^3 of distilled water was added, respectively. The boxes were placed in a dry, shady location in the room (central heating) and

were weighed every day. The decrease in weight was equated with the evaporation of water. Diagram 41, p. 188.

Experiment 159. Daily temperature conditions in soil on limestone and on granite. Dlr Rättvik, from 1700 hours on June 4 through 7 p.m. on June 5, 1946. The observation area situated near Sjurberg is described in detail (p. 181) and illustrated with drawings and a photograph (Figs. 14–16). The vegetation on both sides of the fault fissure (orthoceratite limestone as against granite) was similar, meadow type; *Primula farinosa* and *Carex ornithopoda* were found on both sides of the fissure; the moss *Thuidium abietinum* (det. Frisendahl) also requires limestone. —The day before was quite rainy. The soil was therefore unusually moist, which certainly limited the extreme values of temperature. Diagram 40 (p. 185).

The “Limestone Species”

An Example of the Influence of Existence Factors

112 The great importance of limestone ($CaCO_3$) for *plants* has been known for a long time, and there is a very extensive literature (among others: Thurmann, 1849; Kraus, 1911; Warming and Graebner, 1918, p. 118 ff.; Frödin, 1919; Salisbury, 1920; Tamm, 1921; Mevius, 1921, 1924; Th. Fries, 1925; Arrhenius, 1926; Pesola, 1928; Brenner, 1930; Lundegårdh, 1930, p. 335 ff.; Eklund, 1931, 1933).

Many *animals*, including insects, are often commonly named “limestone species” or at least “limestone favored” species, depending on their more or less pronounced regular occurrence on calcareous soil. In Part I of this work, such contentions or assumptions on my own part or others’ are mentioned with the relevant species.

In Fennoscandia the occurrence of the exposed limestone rock is extremely limited*, and the more or less limestone-rich loose deposits (especially moraine and marl) are very unevenly distributed (maps in Figs. 9 and 10). The species associated with limestone†, if such species occur at all, must therefore occupy a corresponding area. Actually to date it is almost always on the basis of such comparisons and considerations that certain insects are designated “limestone species” in Fennoscandia (and usually elsewhere).

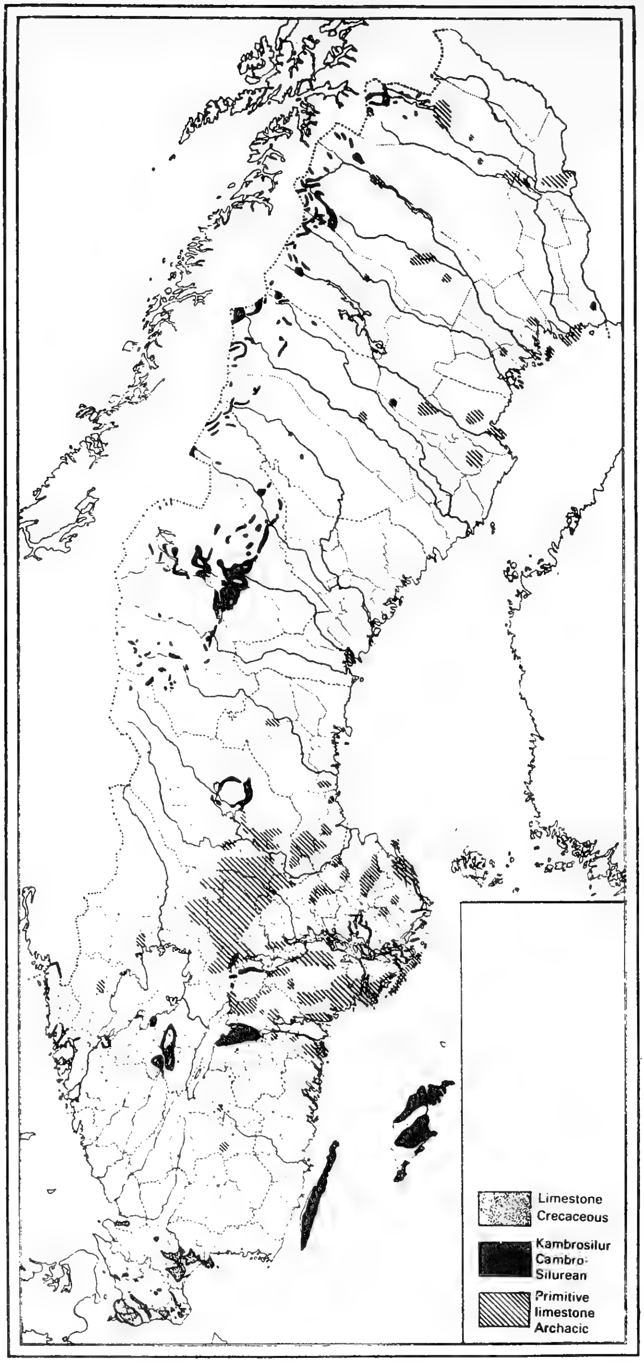
On this basis, there are primarily two geographical groups in our area:

1. Species which in Scandinavia occur in Öland and Gotland: a) restricted to these islands; and b) with their northern limit in one of these islands. Ex-
113 amples: a) *Harpalus azureus, Harpalus punctatulus, Harpalus rupicola***; b) *Cymindis humeralis, Harpalus melancholicus, Harpalus melleti, Harpalus neglectus, Harpalus picipennis, Harpalus serripes, Harpalus servus, Harpalus vernalis, Masoreus wetterhalli, Pterostichus punctulatus*. (cf. p. 455 and species mentioned on following pages).

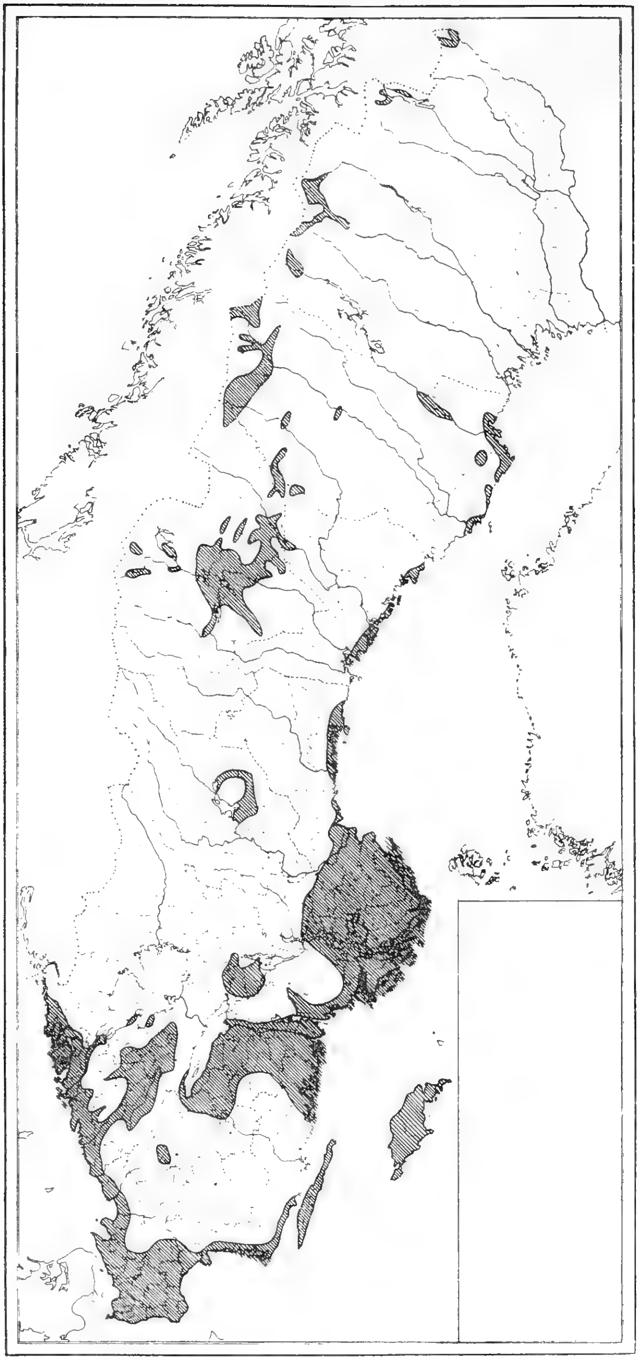
*Siliceous rocks with a greater or lesser limestone content which (as in Värmland) exercise the same influence as limestone, although to a lesser extent (for example, Tamm, 1921, p. 112; Saxén, 1928), are not referred to in the map (Fig. 9).

†(= “calciphilous” species; cf. p. 816; suppl. scient. edit.).

**Besides these three species of *Harpalus*, the only other Scandinavian carabid which has been found only in Öland and (or) Gotland, is *Calosoma investigator* (one specimen).



114 Fig. 9. Compact limestone rock as superstratum in Sweden. Cf. footnote on p. 113. From appendix to "Kalkutredningen" (Sveriges Geol. Unders., 1931; unpublished).



115 Fig. 10. Loose deposits containing limestone in Sweden. After Lundqvist (1925, p. 117; 1943). Actual limits in nature are not so distinct.

2. Species that show a relict-like restricted distribution in or on the small isolated Cambrian-Silurian areas of central Sweden. Examples: *Harpalus anxius, Harpalus rufitarsis, Microlestes minutulus, Panagaeus bipustulatus*; possibly also *Acupalpus consputus, Leistus rufomarginatus, Microlestes maurus*. In Norway the strangely isolated occurrence of *Abax ater* represents a similar case.

On the basis of the distribution pattern alone it is of course not possible to prove that a particular species is associated with limestone, still less to establish which factors operate in this regard. For this reason I decided to study the problem experimentally. Formulation of the problem was simple: it involves the following considerations:

1. *The species in question* were to be examined as thoroughly as possible for their ecology, comparing them with related species with a different mode of life, and also with geographically and ecologically more or less pronounced cosmopolitan species. It was necessary to find any characteristic requirements for life common to the so-called limestone species.

2. *The limestone rock* (especially the Cambro-Silurian) and the limestone-rich loose deposits had to be studied for their chief chemical and physical characteristics, in comparison with siliceous rock (basement complex), which is dominant in Fennoscandia, and siliceous soil.

3. It should be possible to determine *the influence of limestone on the animals* by comparing the results of 1 and 2. If it was possible to correlate the characteristics of "limestone species" and calcareous soil, a causal relationship could be established.

Characteristics of the "Limestone Species"

For several reasons (lack of time, material, etc.) it was impossible to investigate
116 experimentally the limestone requirement of all species. With this limitation it was found advantageous to work with species as closely related as possible, of which it might be assumed that they would not show excessive physiological differences. On the other hand these must include both the well-defined "limestone species" of different types and the ecologically and geographically more or less distinct ubiquists.

These considerations revealed that the genus *Harpalus* would be by far the best for a solution of the problem in hand, the more so because all the three carabid species restricted to Öland and Gotland belong to this genus (subgenus *Ophonus*). In the case of some rare species it was impossible to gather sufficient live material. It was possible to get live material of 15 species, which can be divided into the following 6 groups on the basis of their distribution in Scandinavia (for further details see the maps in Part II):

1. Species restricted to Öland and Gotland:
Harpalus azureus

Harpalus punctatulus
Harpalus rupicola
2. Species whose northern limit in Scandinavia is Öld or Gtl:
*Harpalus hirtipes**
Harpalus melleti
Harpalus neglectus
*Harpalus puncticeps**
*Harpalus serripes**
3. Species with relict-like occurrence in the central Swedish limestone areas:
Harpalus anxius
Harpalus rufitarsis
4. Markedly southern species, but continuously distributed up to northern Upl:
Harpalus rubripes
Harpalus smaragdinus
5. Species with their northern limit in southern Norrland (Mdp):
Harpalus seladon
Harpalus tardus
6. Geographical ubiquist (missing only in the fjelds):
Harpalus aeneus.

The presumed "limestone species" are the 10 species of the first three groups (marked "K" in the reports on experiments in the following pages). The remaining 5 species will be taken into consideration for purposes of comparison.

117 There was also sufficient material of *Harpalus vernalis* (northern limit in Gtl), but this small, sluggish species proved unsuitable for my experiments with the gradient apparatus and is therefore not treated below.

All the species mentioned are animals of open terrain and more or less markedly xerophilous**. The few species of *Harpalus* that deviate ecologically to the extent that they thrive in shady and somewhat moist places (*latus, luteicornis, quadripunctatus, winkleri*), are not considered here, being of little interest.

On the other hand some experiments were carried out with other "limestone species" (along with other species for comparison), including *Amara lucida*, species of *Cymindis*, and *Panagaeus bipustulatus*, some of which are described below.

For an idea of the typical biotopes of the species treated here see the two photographs.

*Only a single more or less accidental locality is known more northerly on the Swedish mainland.

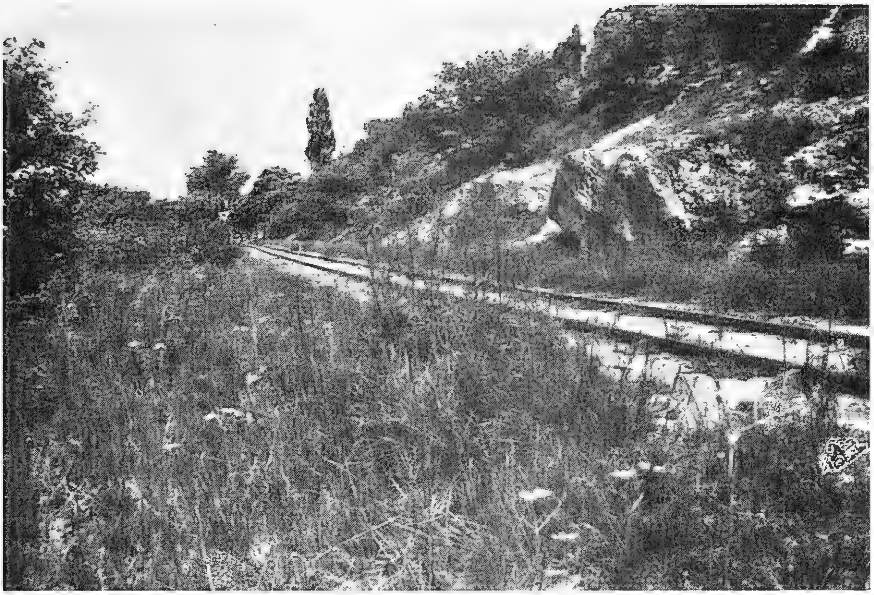
**For *Harpalus aeneus*, see Palmén and Suomalainen (1945).

117 Fig. 11. Öld Räpplinge, southern margin of Greby Alvar, seen from the north. Locality of *Harpalus azureus, H. serripes* and other "limestone species." (Photo: June 15, 1946).

The first of these (Fig. 11) is from Öld Greby (Räpplinge parish) and
118 shows the southern edge of the Greby Alvar[†]. The stony soil on top of the rocky outcrop of the mountain is about 2 dm thick; pH 7.9 (electrometrically measured). The vegetation is very low (partly because of sheep grazing), but is dense and rich in species. The following plants are prominent (regardless of their abundance): *Achillea millefolium*; *Bellis*; *Calamintha acinos*; *Dianthus deltoides*; *Erodium*; *Festuca ovina* and *F. rubra*; *Fragaria viridis*; *Galium verum*; *Herniaria*; *Heiracium pilosella*; *Plantago lanceolata*; *Poa alpina*; *Potentilla argentea*; *Sagina procumbens*; *Sedum acre* and *S. album*; *Thymus serpyllum*; *Trifolium procumbens* and *T. repens*. Solitary shrubs of *Juniperus, Prunus spinosa, Crataegus*, and *Rosa*. Of the species used in experiments the following species lived here: *Harpalus aeneus, H. azureus, H. puncticeps* (1 specimen), *H. rubripes, H. serripes, H. smaragdinus* (2 specimens); *Amara lucida, Cymindis humeralis* (together with *C. angularis*), *Panagaeus bipustulatus*. Other possible "limestone species" are *Agonum dorsale, Brachynus, Calathus mollis, Harpalus vernalis, Ne-*
119 *bria salina*. The curculionid *Lepyrus capucinus* Schall. was common.

The second photograph (Fig. 12) shows the "*locus classicus*" ("typical locality") of *Harpalus rupicola* (Part I, p. 509) near Gtl Visby, a scree slope

[†](A type of rendzina; suppl. gen. edit.).



118 Fig. 12. Gtl Visby. Railroad track embankment south of town, view from the south. Locality of *Harpalus melleti, H. punctatulus, H. rupicola*, and other "limestone species." (Photo: June 9, 1947).

formed by falling weathered gravel, used for a railroad track embankment. The gravel is extremely coarse, mixed with larger stones, and has very high porosity between the particles; pH 7.4 (electrometrically determined). The vegetation is rather sparse but tall. Dominant flora: *Arrhenatherum elatius*; *Centaurea scabiosa, Dactylus glomerata, Daucus, Hieracium* sp., *Medicago sativa*; patchy distribution: *Anthemis tinctoria, Artemisia campestris* and *vulgaris, Cichorium, Potentilla reptans, Ranunculus polyanthemus, Torilis*. Shrubs of *Sorbus suecica*. In addition to *Harpalus rupicola*, also numerous here were *H. melleti* and *H. punctatulus*; *H. aeneus* and *H. rubripes* appeared only sporadically. *Agonum dorsale, Amara curta, Brachynus, Dromius linearis* and larvae of *Licinus* also occurred, among others.

The mineral components of the soil in the two biotopes described above originated from limestone. The admixture of humus is small. In summer the surface layers dry up completely.

The Food

Phytophagous species, dependent on one kind of limestone-bound species of plant, are thereby secondarily associated with limestone. Predatory animals that feed exclusively on phytophagous animals may be considered as the third level of species associated with limestone. It is therefore very important to determine the diet of the suspected "limestone species."

It has been known for a long time that many species of *Harpalus* (and species of *Amara*) are strikingly polyphagous, consuming both vegetable and animal food. As shown elsewhere (p. 531), in this respect they are not exceptional among the carabids, as has been assumed so far, although members of the genus *Harpalus* (and of *Amara*) appear to *prefer* plant food more than other genera. However, they are not fastidious in this respect. The 15 species of *Harpalus* mentioned above (besides *H. vernalis*) used in my experiments, as well as the species of *Cymindis* (*angularis, humeralis, macularis*), *Panagaeus bipustulatus, Brachynus*, and many others, were fed exclusively on bread for many months and were found to thrive (*Harpalus serripes* for more than 3
120 years!). They did not attack living insects (not even small tender ones such as the collembolans) but greedily devoured crushed conspecific individuals and other species of *Harpalus*. At any rate this was established for *H. aeneus, H. anxius, H. punctatulus, H. rubripes, H. smaragdinus* and *H. tardus*. *H. serripes* also consumed a dead *Tenebrio* and *H. hirtipes, H. neglectus* and *H. punctatulus* ate crushed flies. The last named species also accepted a dead *Amara aenea*.

The earlier observations, given in Part I, showed pronounced and spontaneous polyphagy of *H. aeneus, H. calceatus, H. distinguendus, H. pubescens* and *H. puncticeps*. Members of the subgenus *Ophonus* have been observed quite frequently on the umbels of Umbelliferae attacking unripe fruits; there was also spontaneous feeding on seeds of another kind by *H. griseus*.

The above observations apply to adults. Little is known about the nourishment of the larvae; in general they are considered polyphagous carnivores. But the larva of *H. pubescens* is also believed to consume vegetable food.

At any rate it has been established that species of *Harpalus* are not dependent on a particular plant or a particular prey for their nourishment. Their somewhat restricted distribution, due to which it was assumed in certain cases that they require limestone may in no way be due to food habits.

Preferenda Experiments with Limestone

The first main experimental task naturally was to determine how the species in question react to limestone ($CaCO_3$).

The behavior of a series of species toward siliceous gravel was first studied with increasing admixtures of $CaCO_3$ (precipitated chalk) in the substratum

gradient apparatus (devised by Krogerus) (Experiment 31 ff., p. 75; Table 2)*.

None of the 5 species studied revealed attraction to the chalk-rich end of the gradient apparatus.

Since it might possibly be presumed that the animals are able to consume chalk only in dissolved form, the experiment was changed so that in place of
121 pure water, water saturated with CO_2 was added to the soil, in which a smaller or larger amount of chalk was mixed (Experiment 32 ff., p. 76; Table 3). The same 5 species were used.

The result thus obtained showed no striking difference from that obtained earlier: *$CaCO_3$ on its own does not attract the species in question.* But it may seem strange that the animals do not distribute themselves uniformly in the gradient apparatus and instead show a pronounced tendency to congregate in the half that is *poor in chalk.* The reason probably lies in the extremely small particle size of chalk, as a result of which the porosity of the substratum is reduced, and the animals have difficulty burrowing into the substratum. The experiments would therefore have required repetition after the corresponding correction, possibly supplemented with alternating instead of serial experiments, and with much more material. However, this proved unnecessary as a result of the experiments with limestone gravel and siliceous gravel discussed later.

122 It has often been emphasized by botanists that most limestone plants do not require limestone as nutrient (e.g. Lundegårdh, 1930, p. 339), but are on the other hand dependent on factors secondarily caused by limestone or at least usually characteristic of limestone-rich soil. These factors have been summed up by Brenner (1930, p. 85) under the same "complex of limestone factors." "The most important limestone factor for most plants is undoubtedly the relatively neutral and stable reaction"† (l.c.; also cf. Arrhennius, 1926, and Lundegårdh, 1930, pp. 341 ff.). Even though high pH of the soil is not always caused by limestone, this is evidently the most important factor for the neutralization of acids and for geographical distribution of different pH values in soil that is otherwise of the same kind, coinciding to a large extent with the distribution of limestone (both as outcropping rock and in the form of loose deposits) (Fig. 13).

This pH map therefore shows values on the high side (less acidity) in areas with limestone mountains (cf. map in Fig. 9, p. 114) and in those which, starting from the former, are located in the direction of the movement of inland ice, where as a result loose limestone was transported chiefly as moraine. Examples
124 are the areas between Jtl Storsjön lake and the Bothnian sea, and the northern parts of the "Swedish highlands" (Vgl, Små, Ögl). The relatively high pH

*For further details concerning the experiments, reference may be made to the transcript of experiments (p. 66 ff.).

†(="Response"; suppl. scient. edit.).

121 **Table 2. Distribution of 5 species of *Harpalus* in the substratum gradient apparatus on siliceous gravel with different admixtures of $CaCO_3$ (chalk)**

Percentage values refer to volumes. "K"—suspected "limestone species." Experiment 31 ff., p. 75

	Silicate	Silicate +0.78% $CaCO_3$	— 1.56 % —	— 3.13 % —	— 6.25 % —	— 12.5 % —	— 25 % —	— 50 % $CaCO_3$
punctatulus K[2]	2	7	4	3	2	4	2	0
			16			8		
serripes K	5	7	4	2	2	1	1	0
			18			4		
seladon	8	2	3	0	0	0	0	1
			13			1		
rupicola K	6	4	3	6	3	0	0	1
			19			4		
melleti K	7	4	2	3	1	0	1	0
			16			2		

122 **Table 3. As in Table 2, but soil moistened with CO_2-saturated water, Experiment 32 ff., p. 76**

	Silicate	Silicate +0.78% $CaCO_3$	— 1.56 % —	— 3.13 % —	— 6.25 % —	— 12.5 % —	— 25% —	— 50 % $CaCO_3$
punctatulus K	4	13	2	3	0	0	1	0
			22			1		
serripes K	3	2	3	4	2	1	1	2
			12			6		
seladon	3	7	9	1	0	0	0	1
			20			1		
rupicola K	2	5	5	3	4	3	1	0
			15			8		
melleti K	3	2	5	4	2	1	0	0
			14			3		

values of the last-named are somewhat surprising, since this region is poor in flora, primarily due to the shortage of nutrient-rich loam and not because of the pH.

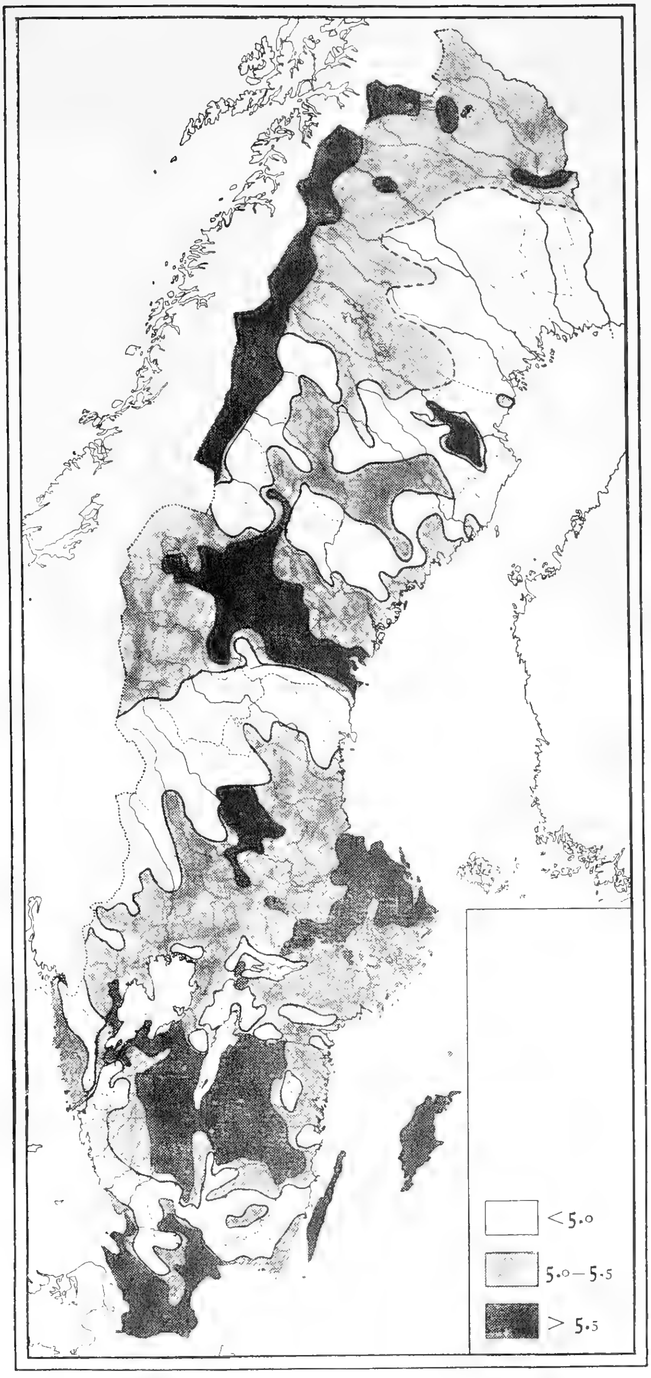


Fig. 13. pH of peat soil. Average values of pH of cultivated bogs. From supplement of "Kalkutredningen" (Sveriges Geol. Unders., 1931; unpublished). Area with higher pH in Vbt is actually somewhat larger.

At any rate it was found absolutely essential to study the behavior of our "limestone species" against different pH values, the more so because Krogerus (1939, p. 1222 ff.) had already shown that the moor fauna comprises various insects, including Coleoptera (also carabids), that are "stenoionic," i.e. intolerant of large variations in soil reaction.

The experiments (Experiment 41 ff., p. 76; Table 4) were carried out with the same 5 species studied with respect to $CaCO_3$, also in the substratum gradient apparatus. The arrangement of the boxes is shown in Table 4; the animals were given the choice of 3 pH values (4.8 and 7.5, and a mixture of both, hence approximately 6.0). The result was expressed as the mean number of individuals per box.

125 It was found that none of the 5 species was attracted to the alkaline sample (pH 7.5). This was all the more surprising in that this soil was taken from a locality of *H. seladon* in Gotland. Therefore at least for this species there was no question of any unfavorable influence of other chemical factors. The pH of the common locality of *H. melleti, H. punctatulus* and *H. rupicola* in Gtl Visby (Fig. 12) was 7.4 and that of *H. serripes* in Öld Greby (Fig. 11) was 7.9. The preference for the acidic samples by all species might be due to the somewhat smaller size of the particles and higher water-storage capacity. However, these differences are not large, and the experiment shows that the (chemical†) reaction of the soil, within given limits, has no demonstrable effect on the species tested.

124 **Table 4. Distribution of 5 species of *Harpalus* in the substratum gradient apparatus with soil of 3 different pH values. Experiment 41 ff., p. 76**

Arrangement of boxes

pH > 6.0	pH 7.5	pH > 6.0	pH 4.8	pH > 6.0

		Mean number of individuals		
		pH 7.5	pH >6.0	pH 4.8
punctatulus K	33 specimens	4.5	2.2	5.5
serripes K	22 specimens	3	4.3	6
seladon	24 specimens	2	4.3	6
rupicola K	46 specimens	2	4	9
melleti K	25 specimens	1	3	12

†(Suppl. Translator).

The small dependence on reaction and characteristics of the ground water is now easily understandable in the case of the more or less xerophilous species. The beetles meet their requirement of water orally (by drinking or feeding), the impermeability of the cuticle of carabids being evident from the virtual absence of cuticular transpiration (Eder, 1940, p. 208). The main food of the species of *Harpalus*, plant seeds, are deficient in water. The losses due to transpiration must be compensated chiefly by drinking (to a lesser extent by consuming other xerophilous animals). But the surface layers of their habitats usually contain no free water, so they depend on rain and especially on nighttime dew, which, before evaporating in the morning, cannot be noticeably influenced by the high pH of the soil. Concerning the undoubted significance of pH for some hygrophilous carabids, see below (p. 527).

The experiments described so far were intended to study the association of "limestone species" with the chemical characteristics of $CaCO_3$. The result was negative. For this reason I conducted experiments (still in the substratum gradient apparatus) to find out whether the species in question are able to distinguish limestone gravel from other kinds of gravel. To exclude inconsequential differences as far as possible, the particle size of the gravel used was always limited to about 3/4 to 4 mm by sifting. Since these experiments must be considered highly significant they were carried out with a considerable number of species (10) and a larger number of specimens (mostly 100 of each species). The 2 kinds of substrata were placed alternately, with an equal number of boxes.

Table 5. Distribution of some species of *Harpalus, Cymindis humeralis* and *Panagaeus bipustulatus* in the substratum gradient apparatus on limestone ("Kalk") gravel and siliceous gravel. Experiment 47 ff., p. 77

	Limestone gravel	Siliceous gravel	
H. punctatulus K	40	60	= 100 specimens
H. serripes K	40	60	= 100 specimens
H. rubripes	41	59	= 100 specimens
Cym. humeralis K	25	75	= 100 specimens
H. azureus K	76	24	= 100 specimens
H. anxius K	80	20	= 100 specimens
H. rupicola K	81	19	= 100 specimens
H. melleti K	83	17	= 100 specimens
H. rufitarsis K	21 (62%)	13 (38%)	= 34 specimens
Pan. bipustulatus K	32 (82%)	7 (18%)	= 39 specimens

126 First, the distribution on limestone gravel and siliceous gravel was studied (Experiment 47 ff., p. 77; Table 5).

On the basis of the experiment, the species studied can be divided into two distinct groups. The first 4 species in the Table (*Harpalus punctatulus, H. rubripes, H. serripes, Cymindis humeralis*) showed no attraction to limestone. On the contrary, at least 59% of the individuals preferred the boxes with siliceous gravel. In contrast, the remaining species (*Harpalus azureus, H. anxius, H. melleti, H. rufitarsis, H. rupicola, Panagaeus bipustulatus*) exhibited a clear preference for limestone; 62–83% of the individuals were found in limestone.

Harpalus punctatulus and *H. serripes* thus seem to be excluded from the species suspected of being "limestone species," which is in fact not surprising. The former has been found during recent years at many places in southern Finland, including the limestone-deficient parts of the southeast (see map in Eskola, Hackman, etc., 1929). Even though it may be an accidental, climatically determined feature these occurrences prove that the species is able to survive for several years on more or less limestone-free soil. *H. serripes* occurs not only on Alvar soil but also on marine and other deposits of sand (Skå, Gtl, Öld Stora-Rör; Central Europe), which are highly deficient in limestone even in Öland (Sterner, 1938, pp. 17, 19–20).

The distinct inclination for limestone gravel shown by the 6 species men-
127 tioned above may give rise to some queries. Is it the chemical or other characteristics of limestone that are decisive in this respect? There *are* such "other" differences between limestone and siliceous stone. For instance, the former is lighter (weight by volume of gravel, including air spaces, when closely packed is 1.4 as against 1.7 for siliceous gravel)* and its particles, produced by the weathering of a kind of stratified rock, are flattened (hence also lighter for a given diameter). There are thus distinct *mechanical* differences between the two kinds of gravel. Such characteristics of the soil can be important for nocturnal soil animals, which must burrow into the ground every morning.

It was therefore important to test the "remaining" 6 species on a kind of gravel possessing mechanical characteristics, identical as far as possible to those of limestone gravel, but limestone-free. I obtained such material in eroded soil from the clay schist of Dlr Boda, Osmundsberg. The "gravel experiment" was repeated with the 6 species mentioned, with schist substituted for siliceous gravel (Experiment 57 ff., p. 78; Table 6).

The result is unequivocal, if surprising. None of the "limestone species" preferred limestone to schist! Only the two species for which the least (and too scanty) material was available showed the same values. The remaining 4
128 species preferred clay schist, apparently because it had more favorable me-

*On the other hand the weight by volume of each kind of gravel *without* air spaces is greater than in the case of limestone, 2.34 as against 2.20. The two kinds of rock used in Experiment 153 had the following values: limestone 2.63, granite 2.65.

Table 6. Distribution of some species of *Harpalus* and *Panagaeus bipustulatus* in the substratum gradient apparatus on limestone gravel ("Kalk") and $CaCO_3$-free clay schist ("Schiefer") gravel. Experiment 57 ff., p. 78

	Limestone gravel	Clay schist	
H. azureus K	40	60	= 100 specimens
H. anxius K	39	61	= 100 specimens
H. rupicola K	30	70	= 100 specimens
H. melleti K	34	66	= 100 specimens
H. rufitarsis K	17 (49%)	18 (51%)	= 35 specimens
Pan. bipustulatus K	16 (47%)	18 (53%)	= 34 specimens

chanical characteristics (weight by volume: 1.27 against 1.40; with even more flat particles. Weight by volume without air spaces: 2.24).

As far as I can see, the preferenda experiments so far described, which were carried out with sufficient material at least in the case of "gravel experiments," showed that limestone attracts the presumed "limestone species" *not because of its chemical, but because of other characteristics*, either mechanical or not manifested in these experiments. However, these assumptions lead to the conclusion that such preferenda experiments are on the whole reliable and a preferendum is also an optimum or at least comes very close to it. Would it not be possible, on the other hand, that the adult beetles exclusively used for these experiments would be indifferent to limestone, whereas the larva would show a certain requirement of limestone? I do not think so. If the beetle shows no positive limestone preferendum (whether or not it requires limestone or not), then there is the obvious danger that the female may deposit her eggs at a place where a larva with a limestone requirement could not live. It is true in this as in all other cases (discussed at greater length on p. 66) that the greater the difference between the preferendum and the optimum, the less viable is the species. And for this purpose a comparison should be made in the first place between the preferendum of the *most active*† stage and the optimum of the *most inactive*†† stage.

Thermal and Hygric Characteristics of "Limestone Species"

Since the experiments described above did not indicate any dependence of the "limestone species" on the chemical characteristics of $CaCO_3$ I proceeded to test other physiological characters of these species. In particular, their responses to temperature and humidity were studied.

†(= "Mobile"; suppl. Translator).
††(= "Immobile"; suppl. Translator).

The *temperature preferenda* were studied (Experiment 11 ff., p. 71) in the usual temperature gradient apparatus (description on p. 66). The temperature of the place chosen by each individual was computed by interpolation and depicted graphically (Diagram 19). It is easiest to draw a comparison between different species by calculating the median preferendum of the total individuals of each species. An idea of the stenothermy (the more or less firm dependence
131 on a definite temperature range) permits calculation of the dispersion, i.e. the mean deviation of individuals from this median preferendum.

The *critical temperatures* ("response points") were determined (Experiment 125 ff., p. 105 ff.) according to the method of Krogerus (1932, pp. 143–146). For each species 3 specimens were tested, and the mean was calculated from the most resistant animals (in each "point"). This prevents displacement of numbers by a diseased or otherwise debilitated individual. A further difference from Krogerus is that I have excluded his "Point 3," since to me it appears impossible to determine exactly the lowest temperature at which the test animals remain active (cf. p. 104). In Diagram 20 the species are arranged in alphabetical order, since they do not show a ranking order for the various reaction (= "response")† points.

The response of the animals to *humidity* was as well investigated, partly by preferenda experiments and partly by determining their resistance.

I obtained the *humidity preferenda* in the substratum gradient apparatus by serial experiments with 7 categories of completely pure sawdust of different moisture contents (Experiment 79). It must be noted that the distribution of the beetles was studied with regard to the moisture content of the substratum, not of the air, because the apparatus was not closed. At least in the four samples with the highest moisture content (4 to 7) the relative humidity of the air between the substratum particles was certainly identical (100%). In the case of the species of *Harpalus* that live subterraneous for most of the day, the humidity of the substratum not only plays a role in the water balance of the animal, but also determines the possibility of burrowing itself, which was especially evident from experiments described elsewhere (p. 505) with sand of different particle sizes (Experiments 94 ff.). This twofold response of the animals undoubtedly reflects an experimental error. However, since it involves ecologically very closely related species, and only *comparative values* were intended, I consider the conclusions justified. The same goes for the reservation on the inevitable larger clustering of animals at the end of the linear gradient apparatus.—For each species, the average place in the series of boxes was calculated. The diagrams (Diagram 21) illustrate the series from the least to the most "xerophilous" species.

In the initial experiments, with comparatively little material, which were
134 carried out during spring (May) (Diagram 22), *serripes* and *punctatulus*

†(Suppl. scient. edit.).

showed equally strong xerophilous characteristics. But the repetition with more material (June through July), however, showed that *serripes* has a much stronger inclination for dry conditions, which undoubtedly correspond better to the actual situation. V. Perttunen, who later took over the material of both species, tested it in a circular gradient apparatus at different levels of relative humidity of the air and found a much higher preferendum in the case of *punctatulus*. However, in this species the humidity preferendum (and so the temperature preferendum) is extremely labile[†] (see above, p. 57 ff.), so that their place in the "ranking list" (Table 7) remains uncertain.

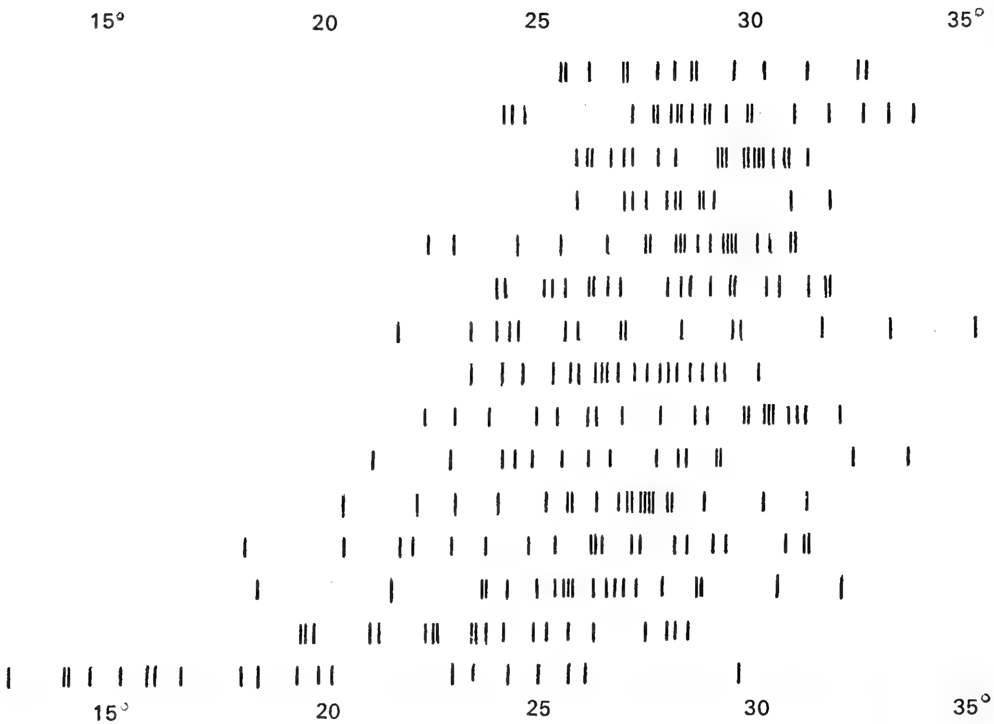
The time the beetle survived in a small dish without water was determined
136 as the relative *resistance to desiccation* (Diagram 23). Three specimens of each species were used. The first indications of paralysis were recorded. As in the case of the "critical" temperatures (Diagram 20), the mean endurance was calculated only from the 2 most resistant individuals. In the diagram (Diagram 23) the species are arranged according to resistance to desiccation.

It is necessary to give a *summary* of the experiments on the response of the species of *Harpalus* to temperature and humidity as described above. It was intended to establish which of these animals are especially *thermophilous* (heat requiring) or *xerophilous* (dryness requiring). The aim of the experiments was to provide only comparative values and it is therefore advisable to consider this summary as a *ranking order* of the species, on the one hand with regard to their thermophily and on the other to their xerophily. However, first of all one must be clear that not all the values obtained are equally significant.

In the temperature studies special importance must be attached to the *mean preferendum*, which shows (excluding experimental errors) the temperature that the species voluntarily seeks out in nature, if possibilities for them are existing. Compared with this, the "mean deviation" from the mean preferendum—the dispersion in the gradient apparatus—is less important. It gives an idea of the relative stenothermy of the species, of the fineness of its temperature sensitivity, and surely also about its persistence in a biotope of a particular temperature type, but not necessarily of a high temperature. For there also exist cold-requiring stenothermous species (Krogerus, 1939, p. 1223). The determination of "critical temperatures" has its greatest importance in that it provides an understanding of the temperature margin within which the species in question remains active, hence about the duration of the annual life period. At any rate, for our climatic conditions it is quite clear that the "lower points" are decisive, i.e. point b (Diagram 20). In this connection, I consider the "upper points" (c, d) rather unimportant. The species studied (with the exception of *H. aeneus*) are nocturnal animals or at least animals of the twilight, which remain buried during the hot day and are not affected by the highest temperatures of the upper layer of soil. As

[†](Ecological term; suppl. scient. edit.).

Species	Specimens	Day of experiment	Mean (temperature)	Dispersion
rufitarsis K	14	25/c	29.36°	2.09°
asureus K	20	21/6	28.95°	2.02°
punctatulus K	20	25/6[1]	28.83°	1.53°
puncticeps K	12	25/6	28.46°	1.19°
rubripes	20	22/6	27.99°	1.88°
serripes K	20	26/6	27.93°	2.13°
neglectus K	15	24/6	27.39°	3.09°
Melleti K	20	25/6	26.98°	1.47°
auxius K	20	21/6	26.97°	2.52°
hirtipes K	15	24/6	26.93°	2.65°
aeneus	20	23/6	26.46°	1.94°
smaragdinus	20	23/6	26.00°	2.92°
tardus	20	22/6	25.98°	2.14°
rupicola K	20	22/6	23.81°	2.33°
seladon	20	3/6[2]	19.54°	4.06°



129 Diagram 19. Distribution of 15 species of *Harpalus* in the temperature gradient apparatus. Experiment 11 ff., p. 71 ff.

[1]Concerning variability of preferenda of *H. punctatulus*, see p. 57 ff.; [2]The early date has probably resulted in low figures for *H. seladon*.

Mean temperature for point b for 2 specimens		Mean temperature for point d for 2 specimens
5.2°	*aeneus*	51.6°
3.4°	*anxius K*	51.0°
8.2°	*asureus K*	51.7°
6.7°	*hirtipes K*	51.1°
7.6°	*Melleti K*	47.8°
4.7°	*neglectus K*	50.0°
7.7°	*punctatulus K*	50.4°
7.8°	*puncticeps K*	50.7°
6.5°	*rubripes*	50.7°
7.2°	*rufitarsis K*	50.6°
8.0°	*rupicola K*	49.5°
6.6°	*seladon*	47.4°
5.8°	*serripes K*	50.1°
4.2°	*smaragdinus*	50.9°
6.7°	*tardus*	51.1°
7.0°	*vernalis K*	49.3°

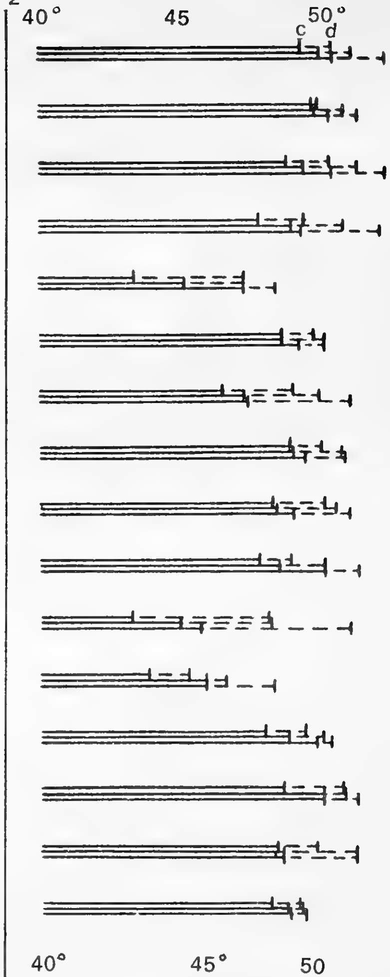
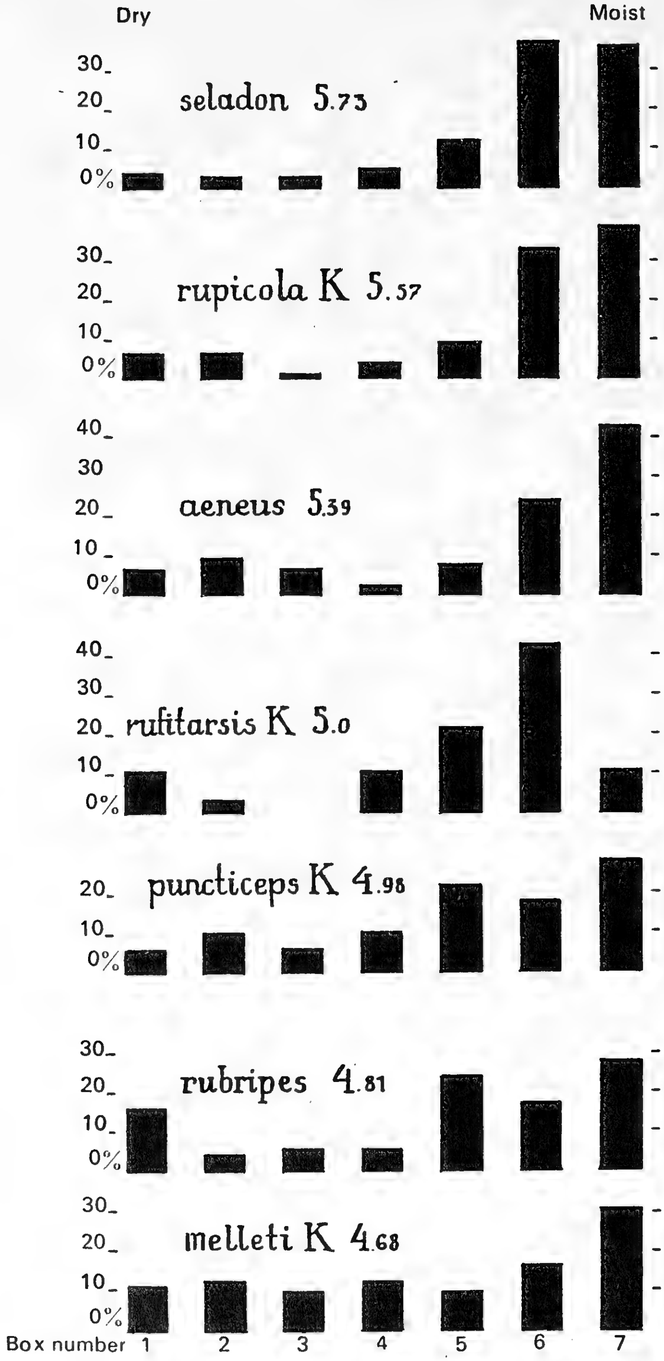
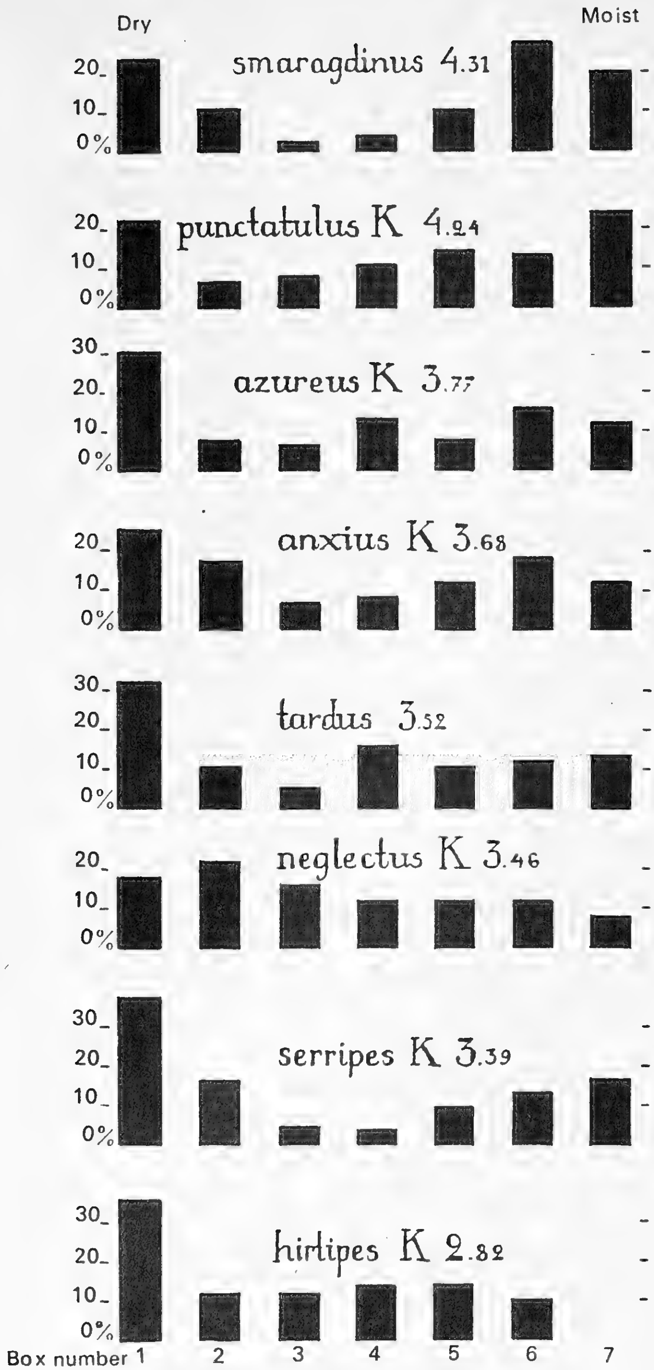


Diagram 20. Temperature response points of 16 species of *Harpalus* (also *H. vernalis,* otherwise not treated). Experiment 125 ff., 132 ff., pp. 105–107.

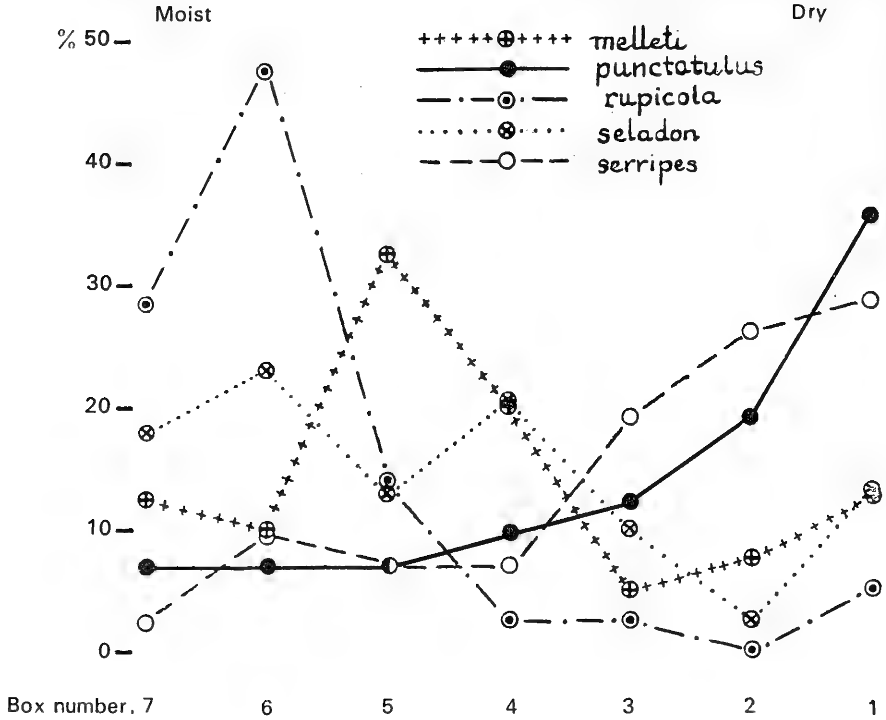
a—First movement; b—Insect has righted itself (= "point of turnover"; suppl. scient. edit.); c—First sign of exhaustion (partial paralysis, especially of hind legs); d—Total heat paralysis.



Dry
Moist
seladon 5.73
rupicola K 5.57
aeneus 5.39
rufitarsis K 5.0
puncticeps K 4.98
rubripes 4.81
melleti K 4.68
30
20
10
0%
40
Box number 1 2 3 4 5 6 7



133 Diagram 21. Distribution of 15 species of *Harpalus* in the substratum gradient apparatus according to varying *moisture*. 7 boxes, number from 1 (dry) to 7 (moist). Calculated "mean box" for each species after name of species. All experiments carried out simultaneously, June 23 through July 24. Experiment 66 ff., p. 79.



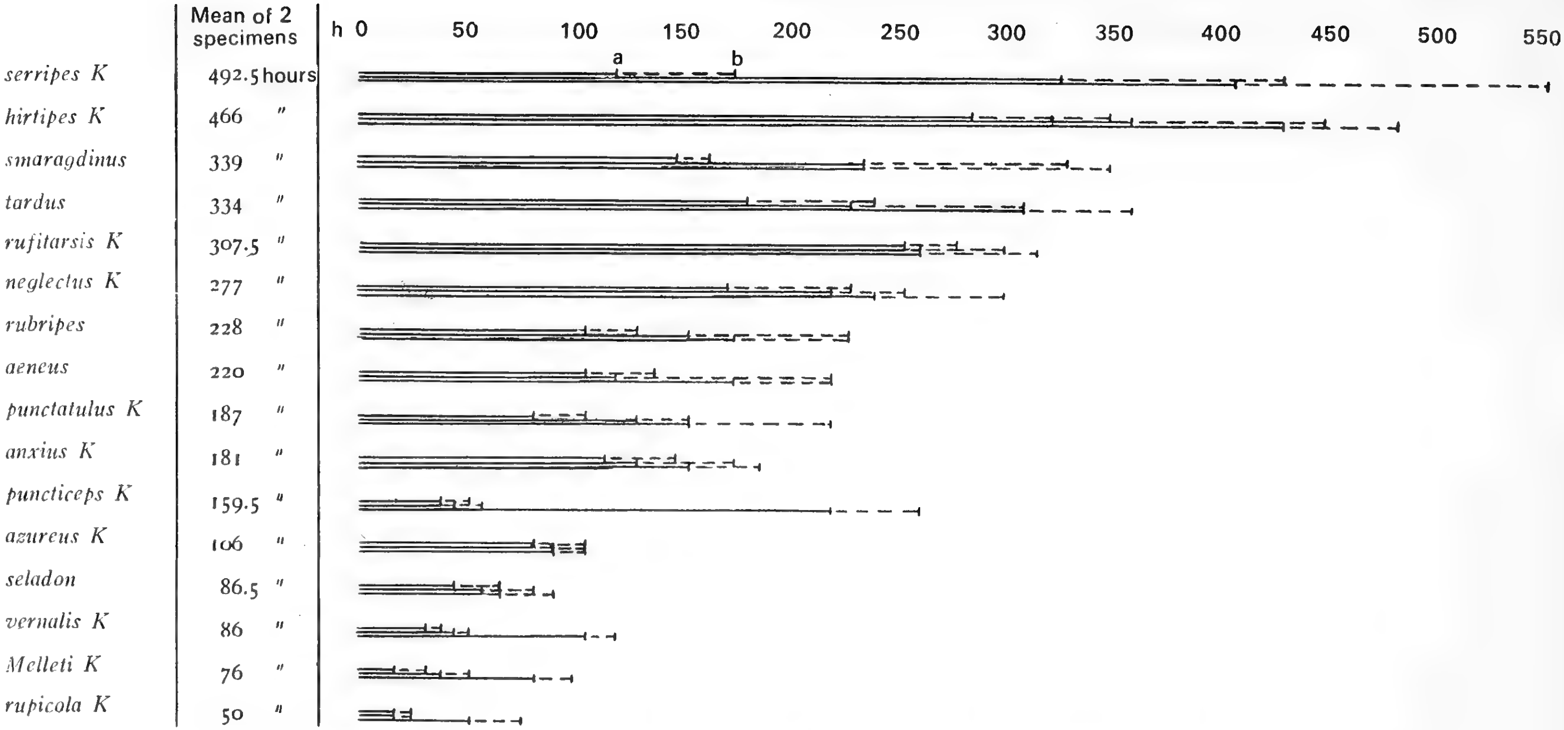
134 Diagram 22. Distribution of 5 species of *Harpalus* in the substratum gradient apparatus according to varying moisture. All species were tested simultaneously, May 19–23. Experiments 70 ff., pp. 79–80. Cf. Diagram 8 (p. 58) and Diagram 21.

far as I am aware, the highest soil temperatures measured in Sweden are from a *Norrlandish pine forest*, where temperature of 59°C was found in the upper
137 mossy layer (Forsslund, 1943, p. 60). Such high values were not even obtained by Kraus (1911, p. 109) in the thermally very favored undulating limestone area in the Maintal†.

In the humidity experiments the *preferenda* should likewise be given priority, partly because they were carried out with more material and partly because the animals in the resistance experiments showed fairly large individual variations.

After long thought I decided to do justice to the very variable significance

†(= valley of the River Main; suppl. translator).



135 Diagram 23. Resistance to desiccation in 16 species of *Harpalus* (also *H. vernalis*, otherwise not treated). Experiments 138–139, p. 108.

a—First sign of exhaustion (partial paralysis or distinct retardation of movements); b—Last time when animal was observed alive.

137 **Table 7. Thermophilous and xerophilous rank of 15 species of *Harpalus* based on experiments. Each of 10 suspected "limestone species" is in bold type in Table where it has a higher position.**

a: mean preferendum and "point b" (Diagram 20, p. 130) calculated twice. b: mean preferendum calculated twice.

	Mean preferendum	Mean deviation from preferendum	Lower temperature limit "point b"
1 **azureus** K	2	6	1
2 **puncticeps** K	4	1	3
3 **punctatulus** K	3	3	4
4 **rufitarsis** K	1	8	6
5 **melleti** K	8	2	5
6 **rupicola** K	14	10	2
7 *rubripes*	5	4	10
8 *tardus*	13	9	7
9 *hirtipes* K	10	12	8
10 *serripes* K	6	7	11
11 *aeneus*	11	5	12
12 *seladon*	15	15	9
13 *neglectus* K	7	14	13
14 *anxius* K	9	11	15
15 *smaragdinus*	12	13	14

	Mean preferendum	Resistance to desiccation
1 **hirtipes** K	1	2
2 **serripes** K	2	1
3 **neglectus** K	3	6
4 *tardus*	4	4
5 *smaragdinus*	8	3
6 **anxius** K	5	10
7 *punctatulus* K	7	9
8 *azureus* K	6	12
9 *rubripes*	10	7
10 *rufitarsis* K	12	5
11 *melleti* K	9	14
12 *puncticeps* K	11	11
13 *aeneus*	13	8
14 *rupicola* K	14	15
15 *seladon*	15	13

138 of the experiments as follows: The "*thermophilous rank*" was calculated from the series of species with respect to cold resistance (Diagram 20, point b), mean preferendum, and mean deviation therefrom (Diagram 19), so that the two first-mentioned values were counted twice. The heat resistance (Diagram 20, points c, d) was not taken into consideration. The "*xerophilous rank*" was determined in the series with regard to the preferendum (Diagram 21) and resistance (Diagram 23, point b), and the former was counted twice.

The result is evident from the two preceding Tables (Table 7a, b). Each of the 10 suspected "limestone species" (groups 1–3, p. 117) is printed in bold face in the Table where it is ranked higher. It is noticeable that the first three positions in both Tables are taken by "limestone species", none of them rank lower than the 6th position in either Table.

We speak of "*xerothermic*" species, i.e. animals which require both warmth and dryness. Evidently it would be possible to prepare a common "xerothermic table" on the pattern of the above Tables. However, data produced as a result of an admixture of diverse characters and viewpoints can hardly be satisfactory. It is more wise to treat each parameter separately. Accordingly the conclusions based on the experimental results can be expressed as follows: *Some of the species of (Harpalus) presumed to be associated with limestone*† *on the basis of their ecological or geographical distribution are markedly heat requiring (thermophilous), whereas others are markedly dryness requiring (xerophilous).*

139 *Cymindis humeralis* is also a distinctly thermophilous species. Its preferred temperature is much higher than in *angularis* and *macularis* (Diagram 24), and shows a very small dispersion. The mean lower and mean upper limit of activity (as calculated in Diagram 20) respectively is: *humeralis* +2.1° and 48.1°; *angularis* +5.4° and 45.4°; *macularis* +2.4° and 47.3°C (Experiments 125, 127, 134, 136, pp. 105 ff.). Resistance to desiccation (as in Diagram 23): *humeralis* 98½; *angularis* 88½; *macularis* 86 hours (Experiments 138, 139, p. 108).

Experiments with the "Universal Gradient Apparatus"

If, as in the preceding section, the effect of two or more factors on one species is studied one of course wishes to compare the degree of their influence on the animal. For instance, if a species exhibits distinct thermophily as well as xerophily the question arises whether the two responses have equal magnitude or whether one is stronger. It is therefore necessary to experimentally test the *simultaneous* influence of two, three or more factors in various combi-

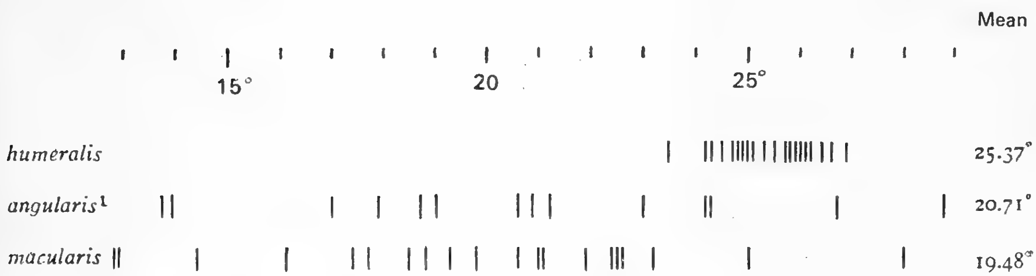


Diagram 24. Distribution of 3 species of *Cymindis* in the temperature gradient apparatus. Experiments 8–10, p. 70. Values for *C. angularis* are certainly too high, because moist cotton was used at the warm end.

†(= "calciphilous species; cf. p. 816; Suppl. Scient. Edit.)

nations. For this purpose I modified Krogerus' apparatus described elsewhere (p. 85), which then received the rather pretentious name "universal gradient apparatus."

In the study of those "limestone species" that are rather insensitive to chemical factors, it was found advisable to restrict the experiments to temperature, humidity and light factors. First, each of these factors was studied separately in the apparatus, and then in different combinations of two or three factors. Each species was therefore subjected to 13* different experiments in the universal gradient apparatus, and each experiment was repeated at least twice (each time with 20 or more specimens). Sufficient living material was not available simultaneously for all 15 species of *Harpalus* treated in the "limestone experiments." The experiments in the universal gradient apparatus were restricted to the following 11 species:

H. aeneus	*H. rupicola*
H. anxius	*H. seladon*
H. azureus	*H. serripes*
H. melleti	*H. smaragdinus*
H. punctatulus	*H. tardus*
H. rubripes	

140 Even this resulted in 154 (11 × 14) different experiments, which can be represented only by as many different diagrams. I was undecided for a long time whether publication of all these diagrams might not be considered a waste of space, since only a small number of them are significant in the present context. On the other hand singularity of behavior of one species under the influence of a given combination of factors can be meaningful only when compared with a sufficient number of "normal" species. Finally, it was possible that useful conclusions might be drawn by other researchers from the basic data I did not utilize.

I therefore decided to publish all the experiments carried out with the help of the universal gradient apparatus in the form of diagrams (Diagrams 25–35).

The 2–4 identical experiments (with the same species) were combined in one diagram and depicted by different types of circles (open, filled, crossed, etc.). Like this, one can always look up the readings for a particular experiment and to some extent draw inferences as to whether the species concerned behaved consistently or not vis-a-vis the particular constellation of factors. A "mean distribution curve" was derived by joining all the values simultaneously obtained (in the same experiments) and subsequent interpolation.

The response to *temperature* was studied by transforming the substratum gradient apparatus into a temperature gradient apparatus (details on p. 86).

*Actually 14 experiments each, since the temperature factor was studied partly with dry and partly with uniformly slightly moist sawdust.

This differed from the usual apparatus only in that it was not possible to read off the actual location of each individual. The beetles were classified according to the number of boxes in 10 temperature categories (Krogerus, 1937, p. 299), whose mean temperature was calculated.

The *humidity* can be equated with the humidity of the substratum. As in the experiments described above (p. 78) on humidity preferenda, sawdust of varying moisture content was spread on the bottom of the boxes in a layer about 5 mm thick. The humidity of the air was subject to much less alteration (p. 88).

The *light* was regulated through squares of different sizes cut out of the black, opaque paper lid (four per box). All the experiments with light were carried out in the laboratory in broad, but indirect daylight (from June 20 through August 1), never under an overcast sky. Since in itself the light factor
174 was of no significant interest for these experiments, being used chiefly to regulate the other two factors, its somewhat variable intensity due to cloud or time of day may be of no great importance. —All experiments in which the light factor was not taken into consideration were carried out in darkness.

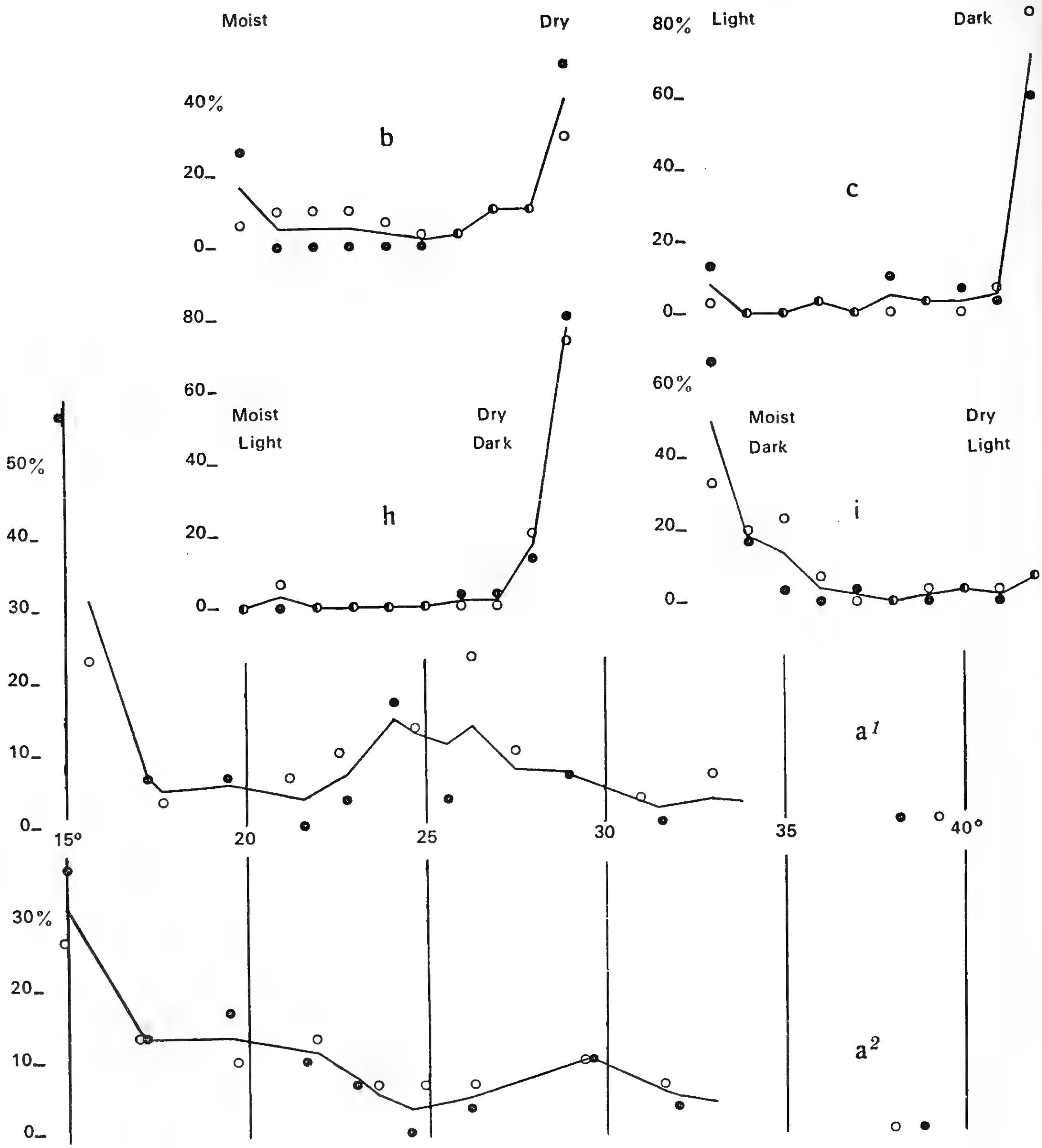
Both, humidity and light were always regularly graded from one end of the gradient apparatus to the other.

An exhaustive discussion on the conclusions that can be drawn from the experiments with the universal gradient apparatus would not be relevant here. I shall therefore restrict myself to a few points which may be important for the "limestone problem."

Since we are dealing with more or less markedly thermophilous, xerophilous and heliphobous animals, in the following account I use the term *similarly directed* factors for two-factor and three-factor experiments, as long as the same end of the apparatus is *warm, dry* and *dark* or any two of these. Otherwise I use the term *differently directed* factors. Admittedly, these terms do not quite fit certain species, for instance, *melleti, rupicola* and *seladon*, which are not markedly xerophilous.

It is clear that the results of the experiments depicted graphically in the diagrams represent only a very general expression of the responses of the species concerned. The experimental material (mostly 40–80 readings) is too small for the plots to be considered authentic in detail. This is especially true of the plots with two or more peaks. On the other hand some species show an astonishing consistency in the position of the maximum, over several (repeated or related) experiments, examples of which are given below. The intention was not to establish the exact distribution of the animals in one or other experiment, but to find the relative changes produced by a new or converse factor.

It is advisable to begin with a comparison of two especially pronounced types, on the one hand *H. azureus*, which in the above correlated temperature



141 Diagram 25 a–c, h–i. *Harpalus aeneus*. Universal gradient apparatus. Experiment 108 (p. 96). a^1—Temperature (dry); a^2—Temperature (slightly moist); b—Humidity; c—Light; h—Humidity + light; i—Humidity – light (cf. p. 176).

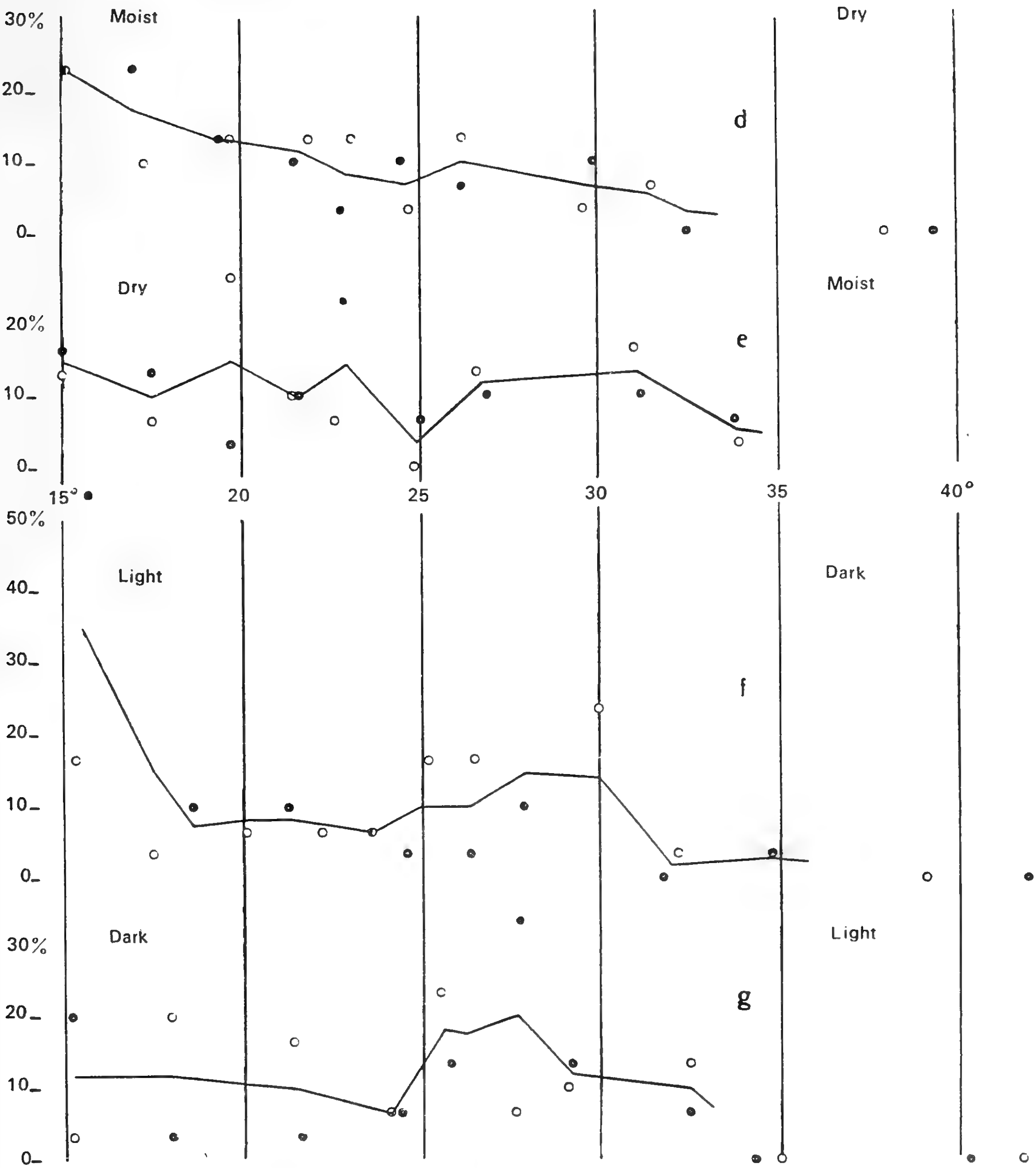
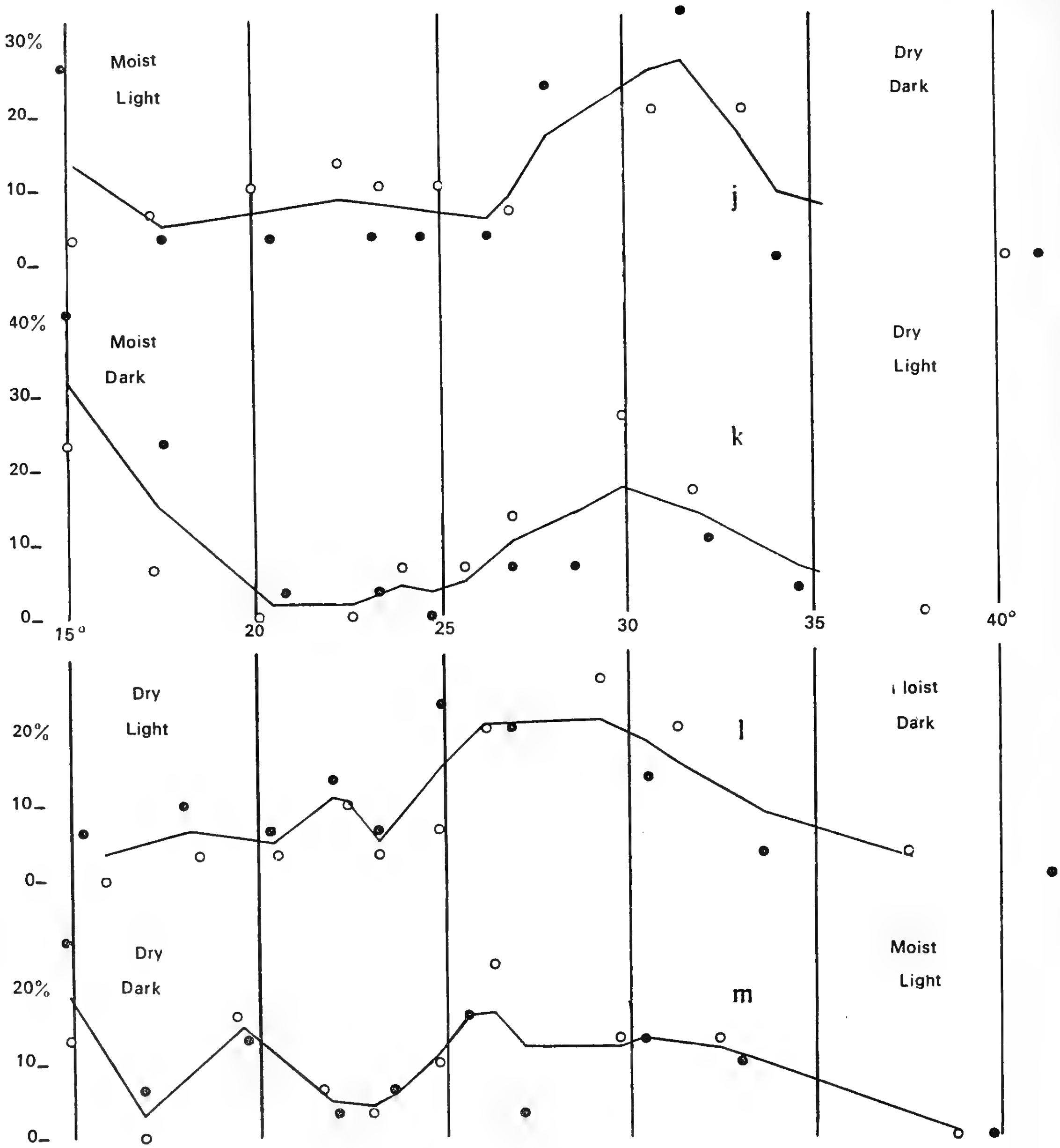


Diagram 25 d–g. *Harpalus aeneus*. Universal gradient apparatus. Experiment 108 (p. 96). d—Temperature + humidity; e—Temperature – humidity; f—Temperature + light; g—Temperature – light (cf. p. 176).



143 Diagram 25 j–m. *Harpalus aeneus*. Universal gradient apparatus. Experiment 108 (p. 96). j—Temperature + humidity + light; k—Temperature + humidity–light; l—Temperature – humidity + light; m—Temperature – humidity–light (cf. p. 176).

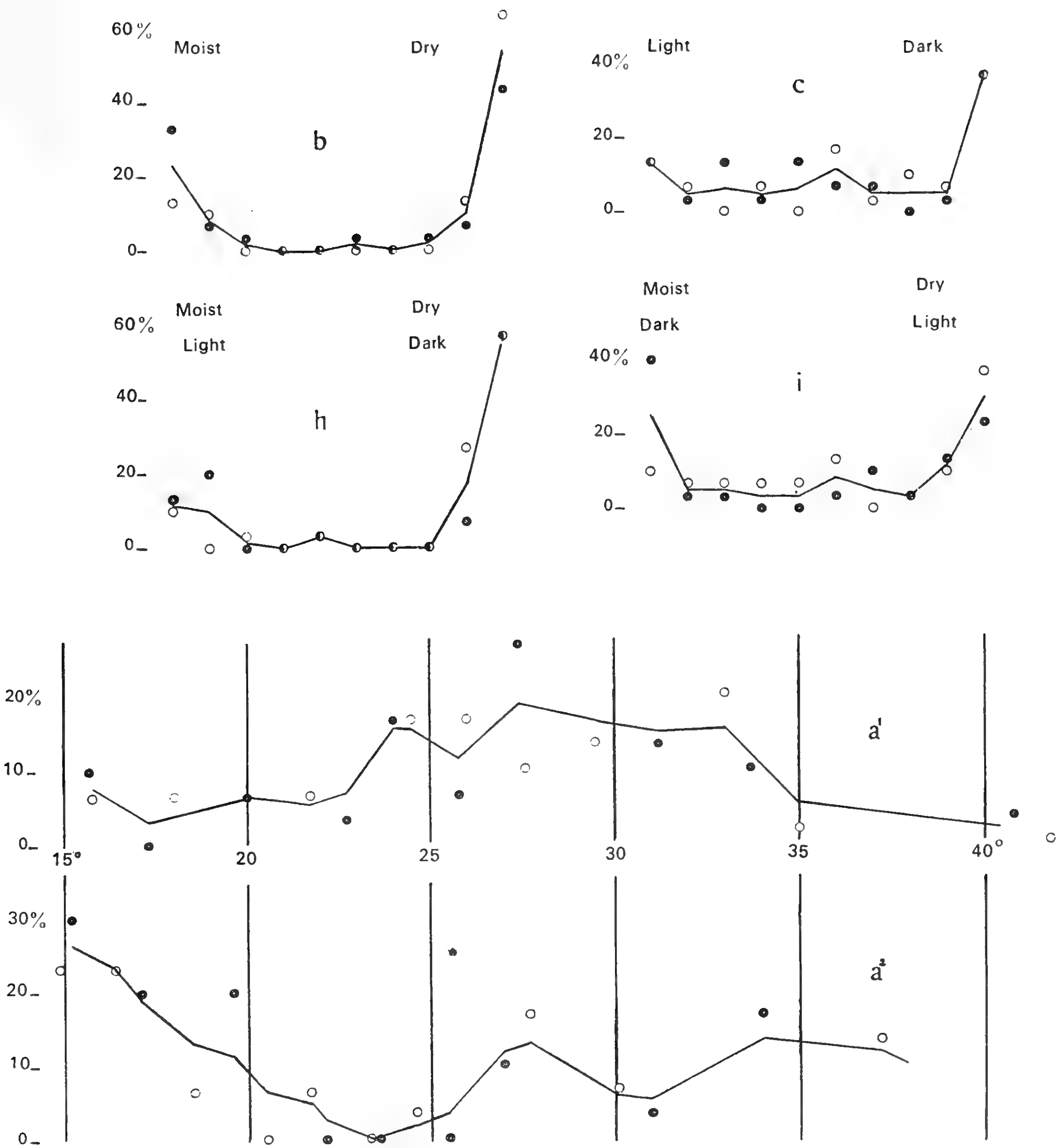


Diagram 26 a–c, h–i. *Harpalus anxius*. Universal gradient apparatus. Experiment 109 (p. 97). See Diagram 25 and p. 175.

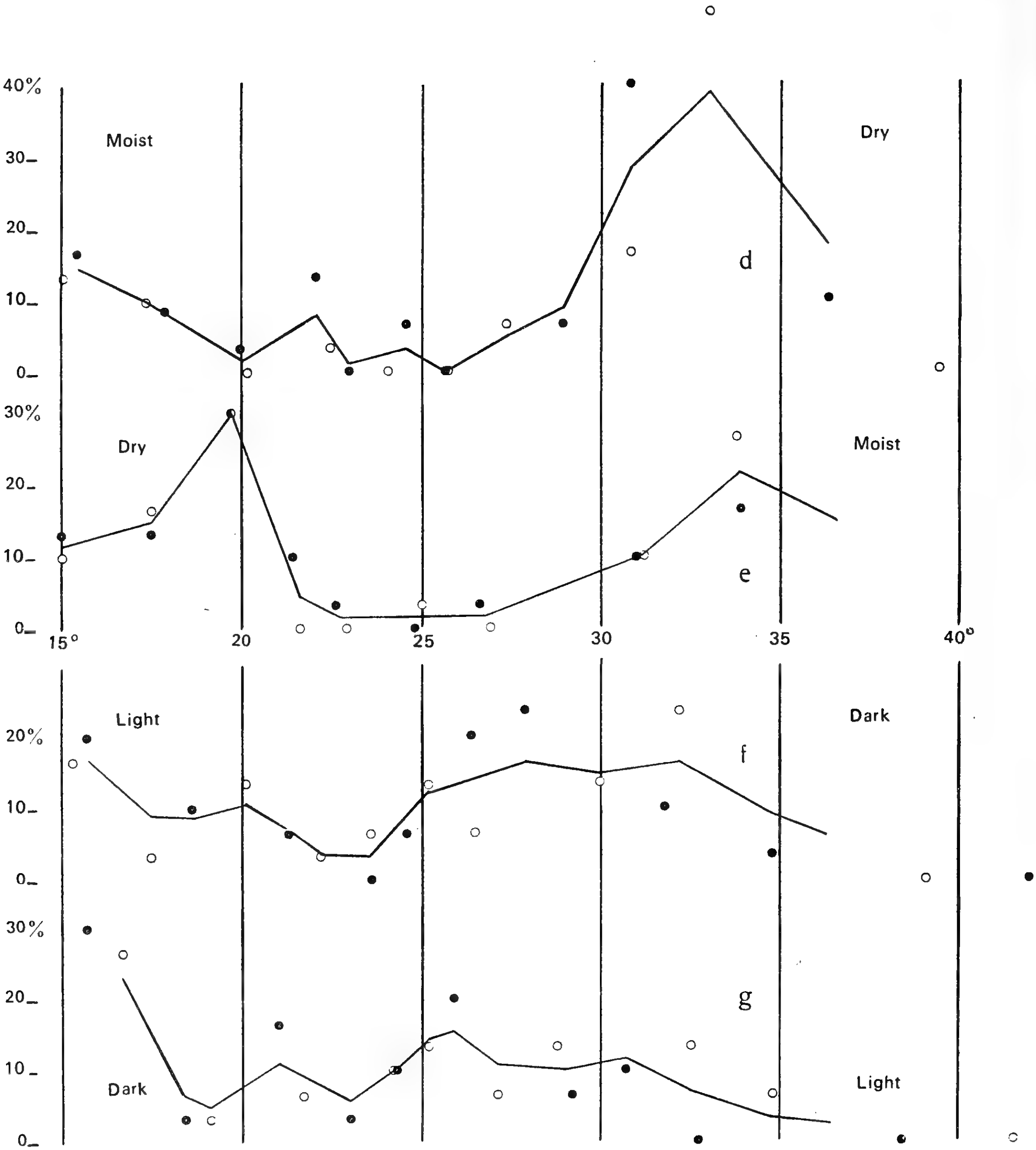


Diagram 26 d–g. *Harpalus anxius*. Universal gradient apparatus. Experiment 109 (p. 97). See Diagram 25 and p. 175.

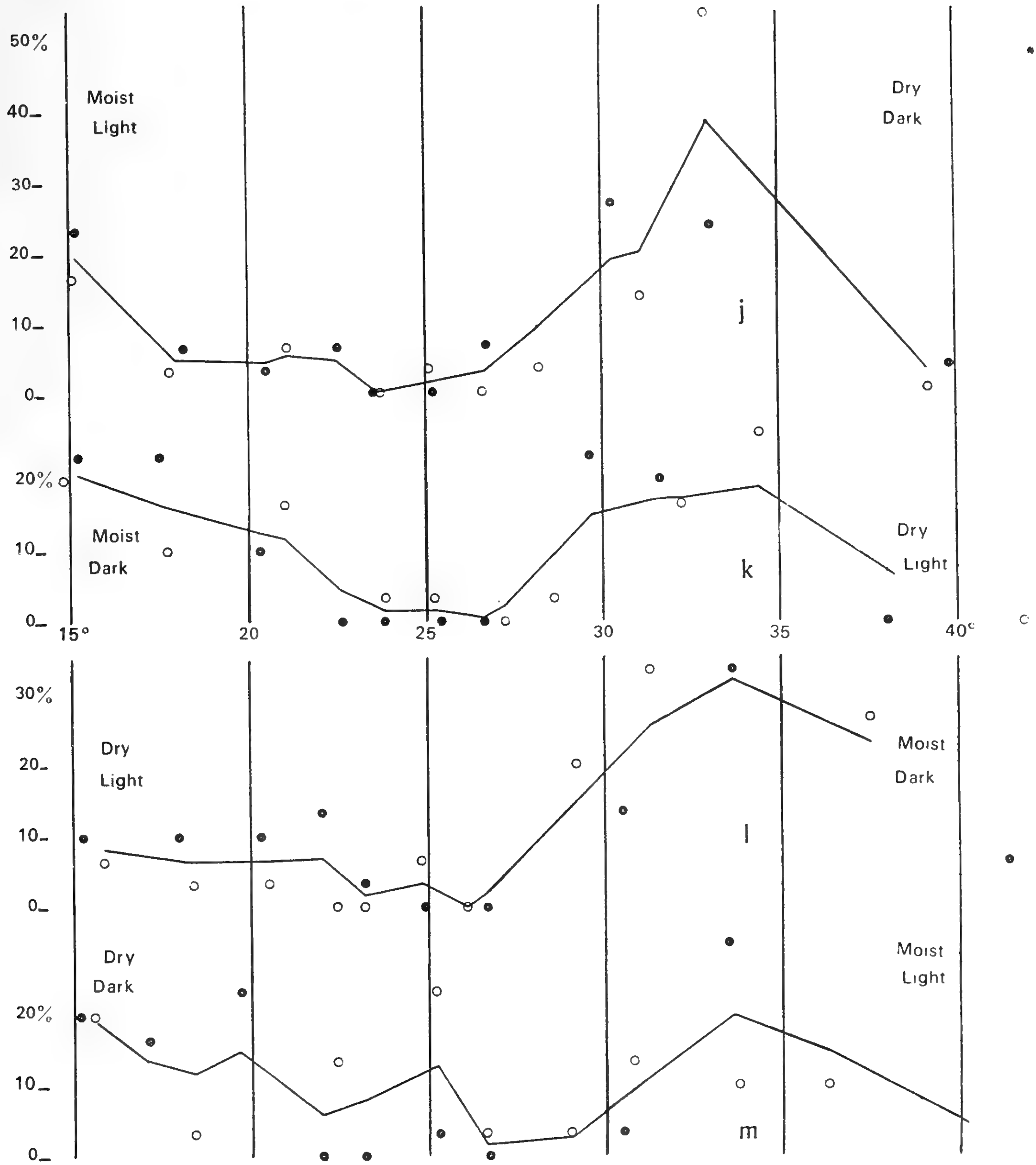


Diagram 26 j–m. *Harpalus anxius*. Universal gradient apparatus. Experiment 109 (p. 97). See Diagram 25 and p. 175.

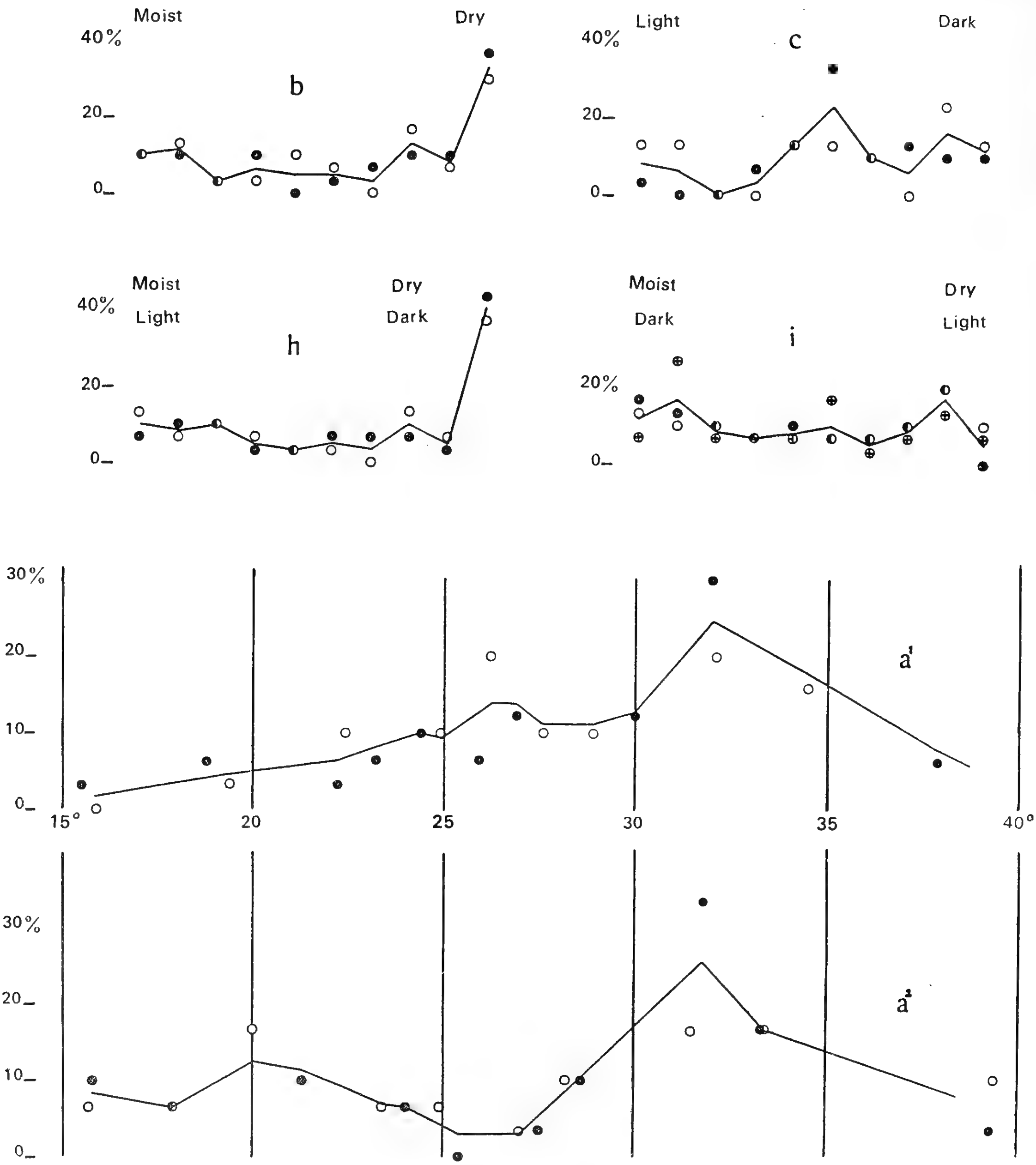
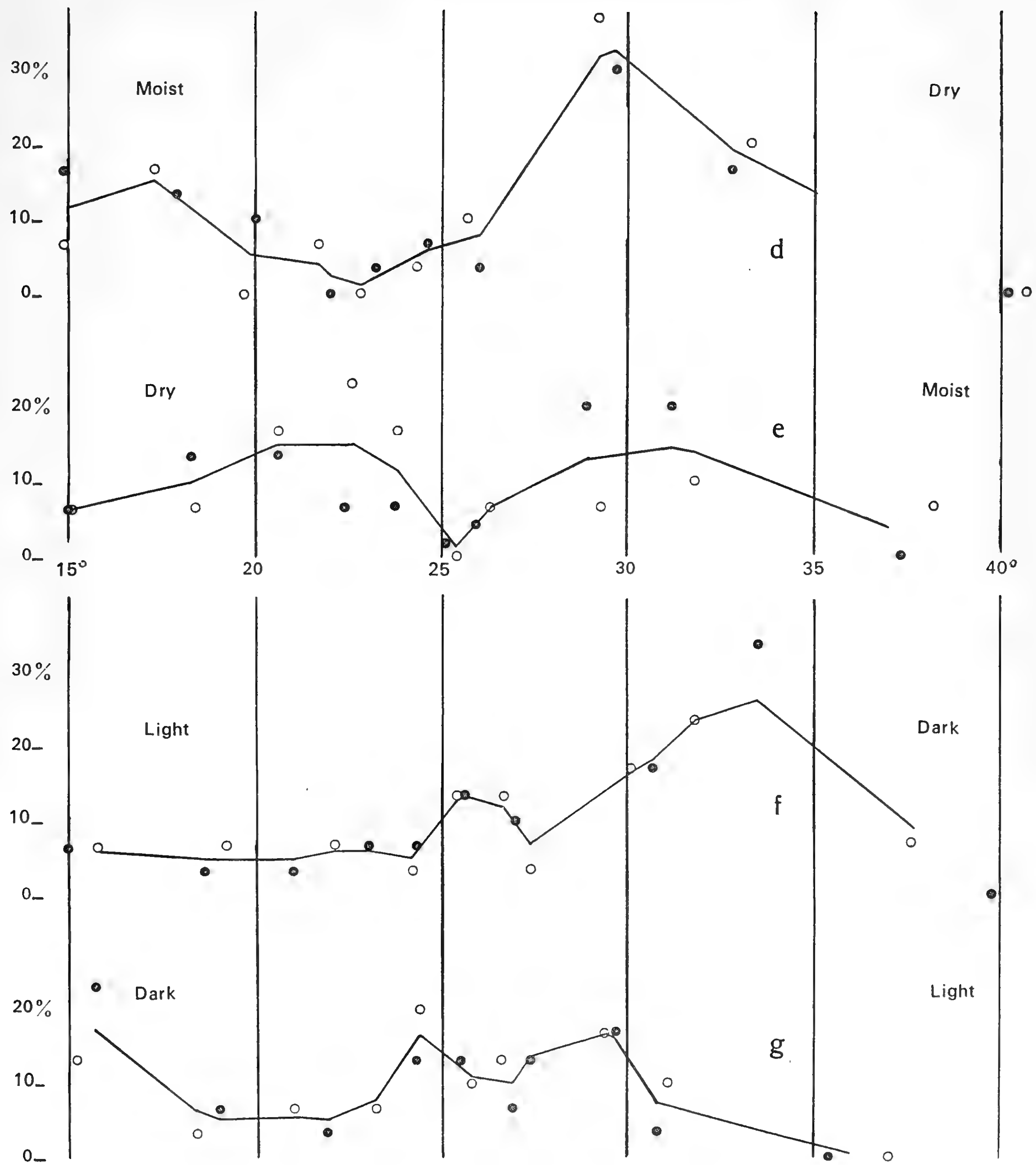


 Diagram 27 a–c, h–i. *Harpalus azureus*. Universal gradient apparatus. Experiment 110 (p. 97). See Diagram 25 and p. 174.



148 Diagram 27 d–g. *Harpalus azureus*. Universal gradient apparatus. Experiment 110 (p. 97). See Diagram 25 and p. 174.

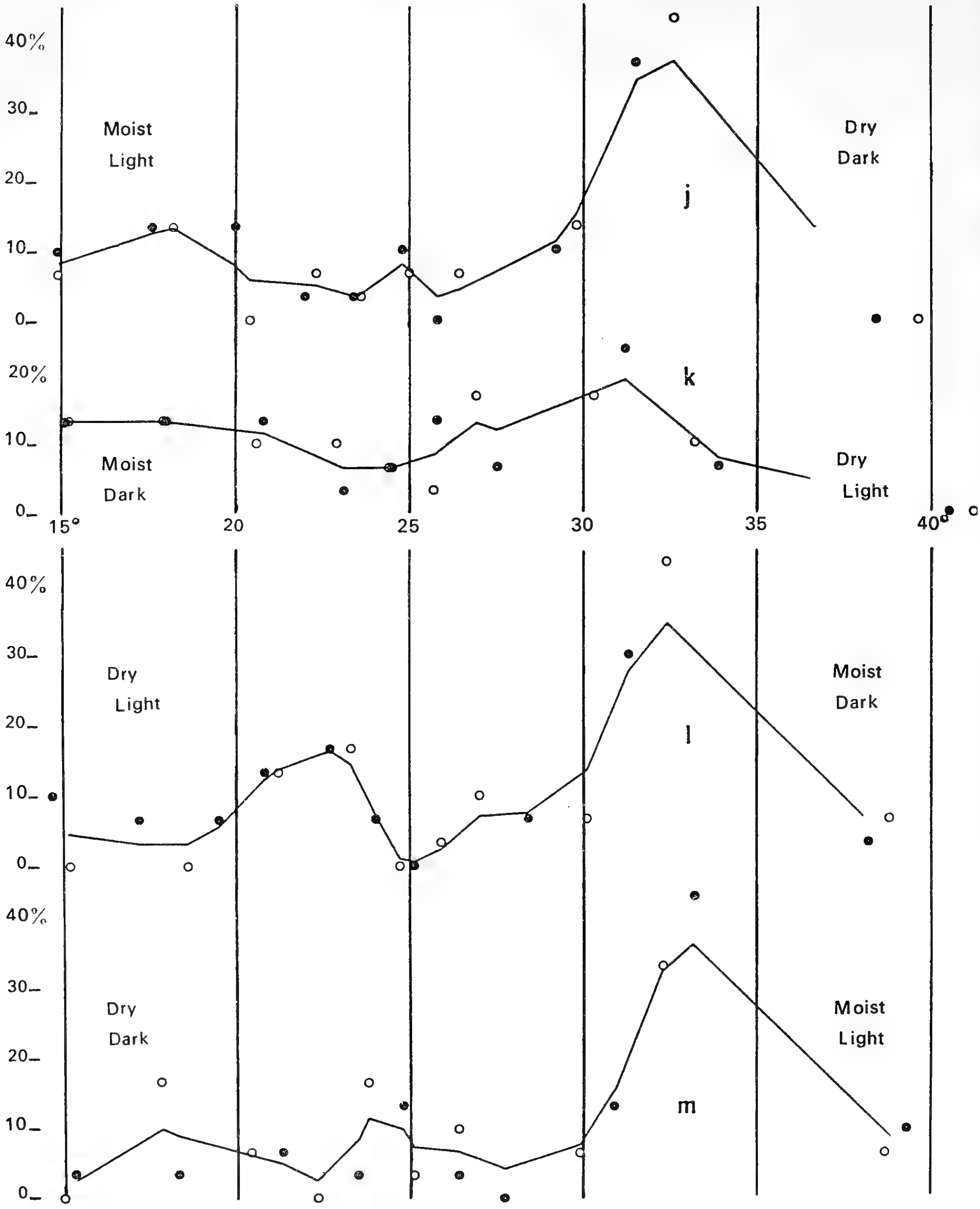


Diagram 27 j–m. *Harpalus azureus*. Universal gradient apparatus. Experiment 110 (p. 98). See Diagram 25 and p. 174.

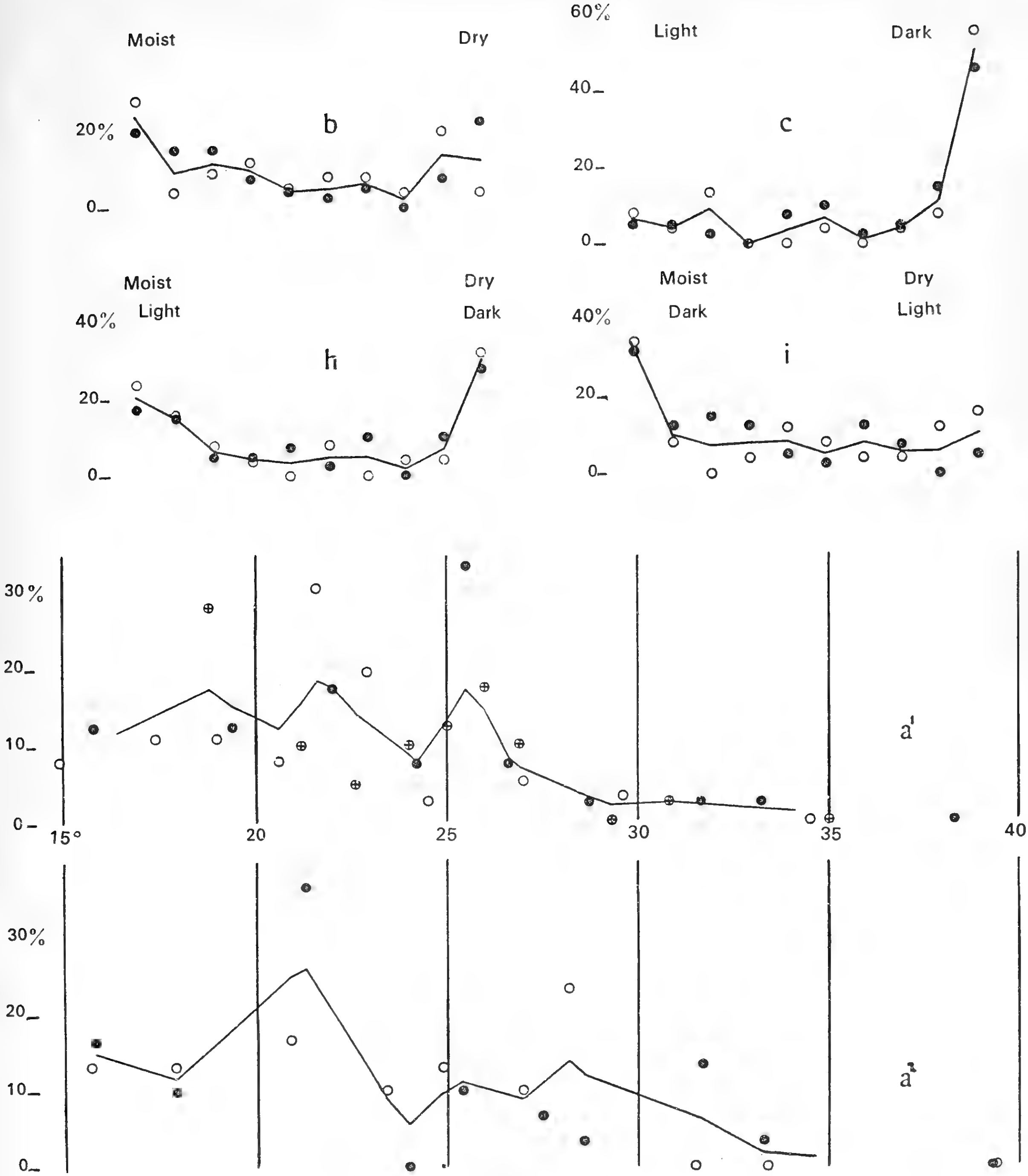


Diagram 28 a–c, h–i. *Harpalus melleti*. Universal gradient apparatus. Experiment 111 (p. 98). See Diagram 25 and p. 176.

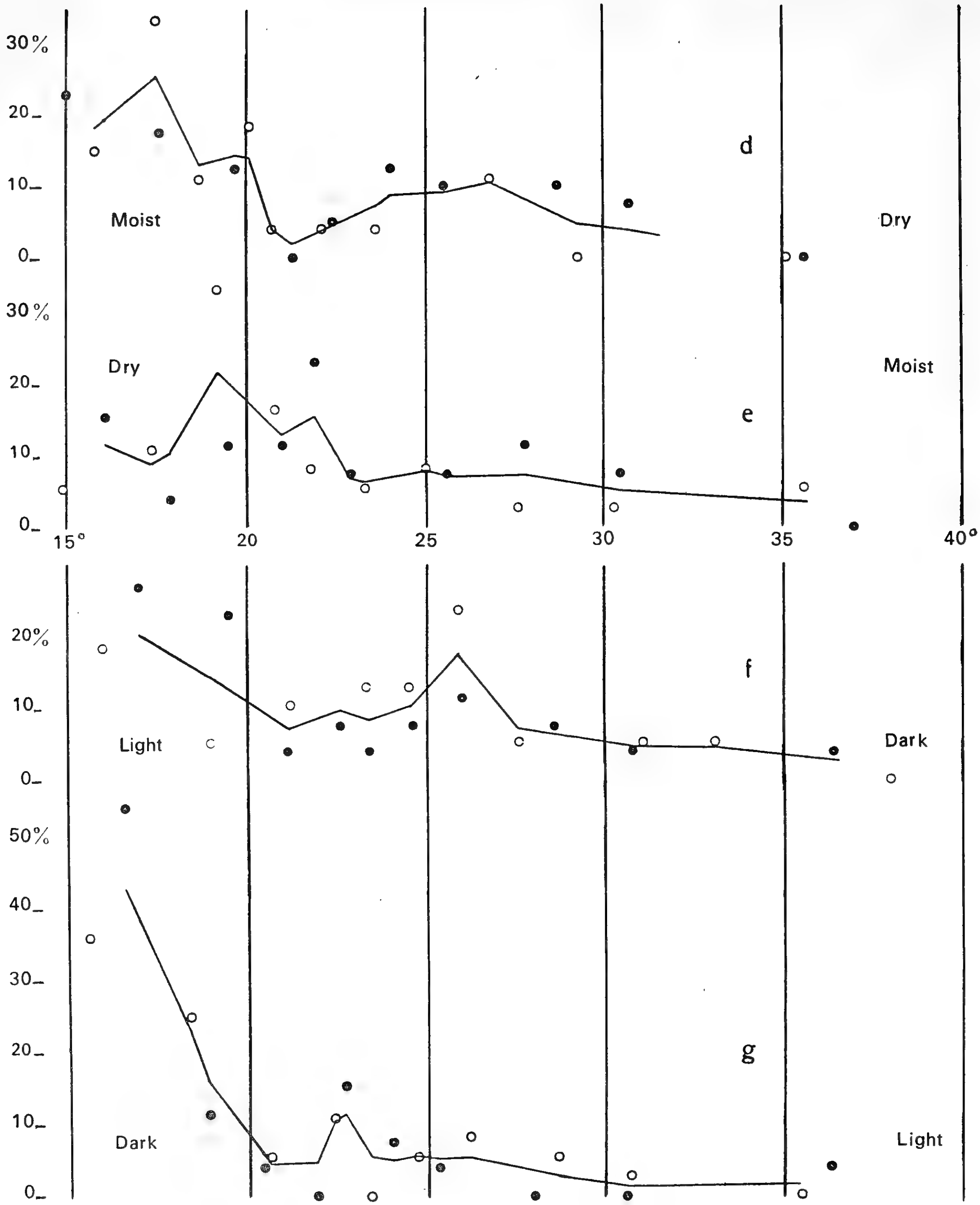


Diagram 28 d–g. *Harpalus melleti*. Universal gradient apparatus. Experiment 111 (p. 98). See Diagram 25 and p. 176.

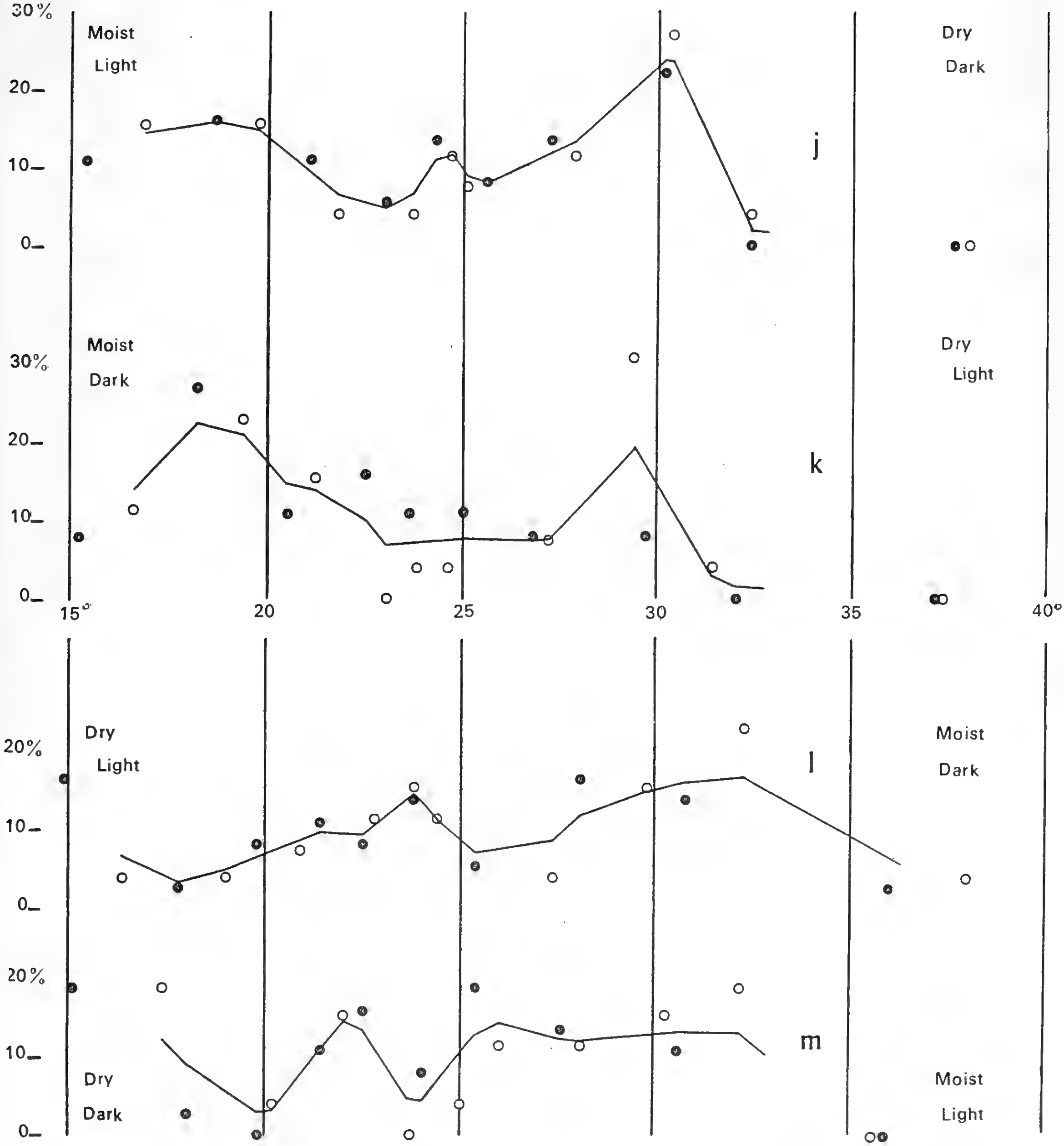


Diagram 28 j–m. *Harpalus melleti*. Universal gradient apparatus. Experiment 111 (p. 98). See Diagram 25 and p. 176.

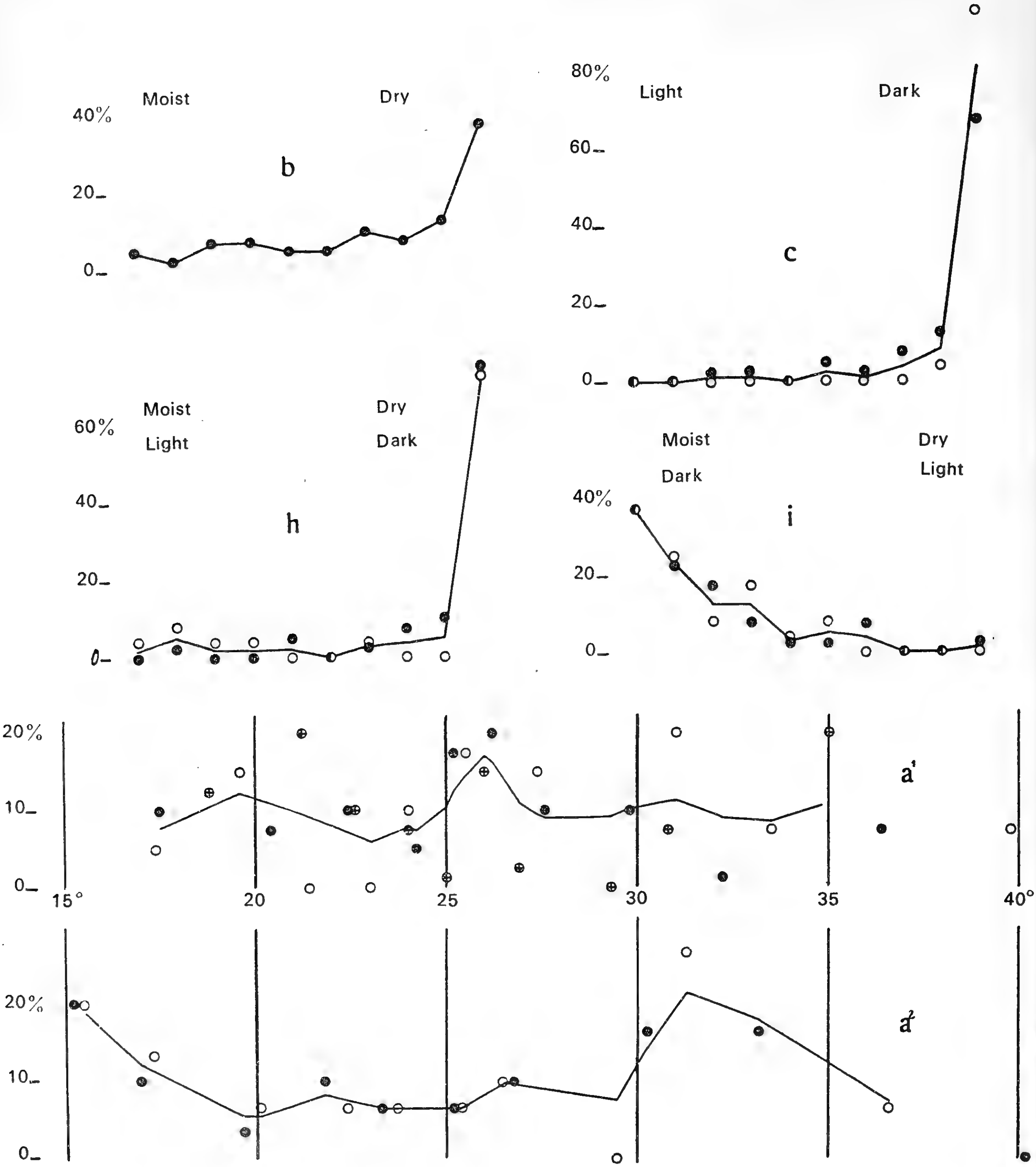


Diagram 29 a–c, h–i. *Harpalus punctatulus*. Universal gradient apparatus. Experiment 112 (p. 98). See Diagram 25 and p. 175.

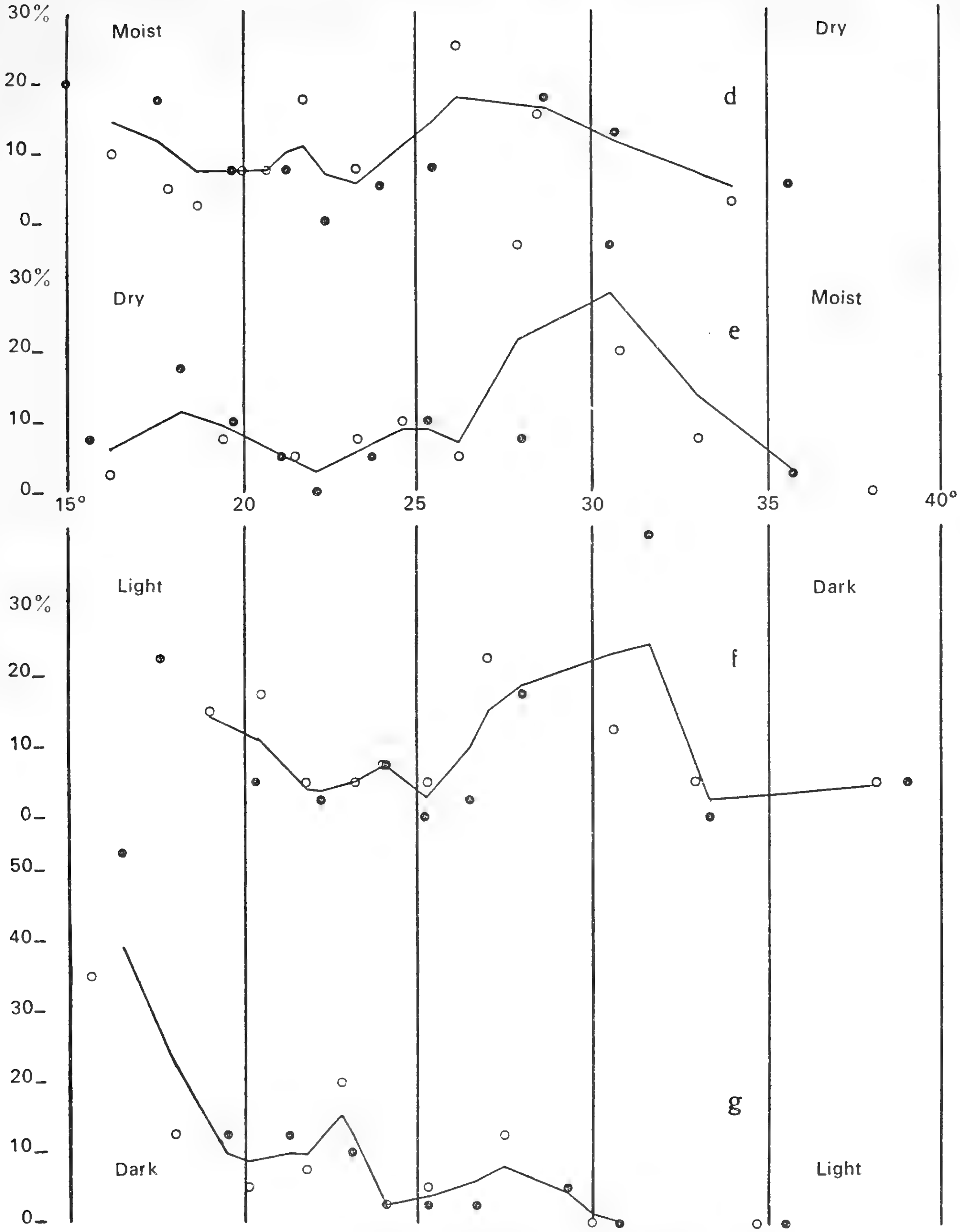


Diagram 29 d–g. *Harpalus punctatulus*. Universal gradient apparatus. Experiment 112 (p. 99). See Diagram 25 and p. 175.

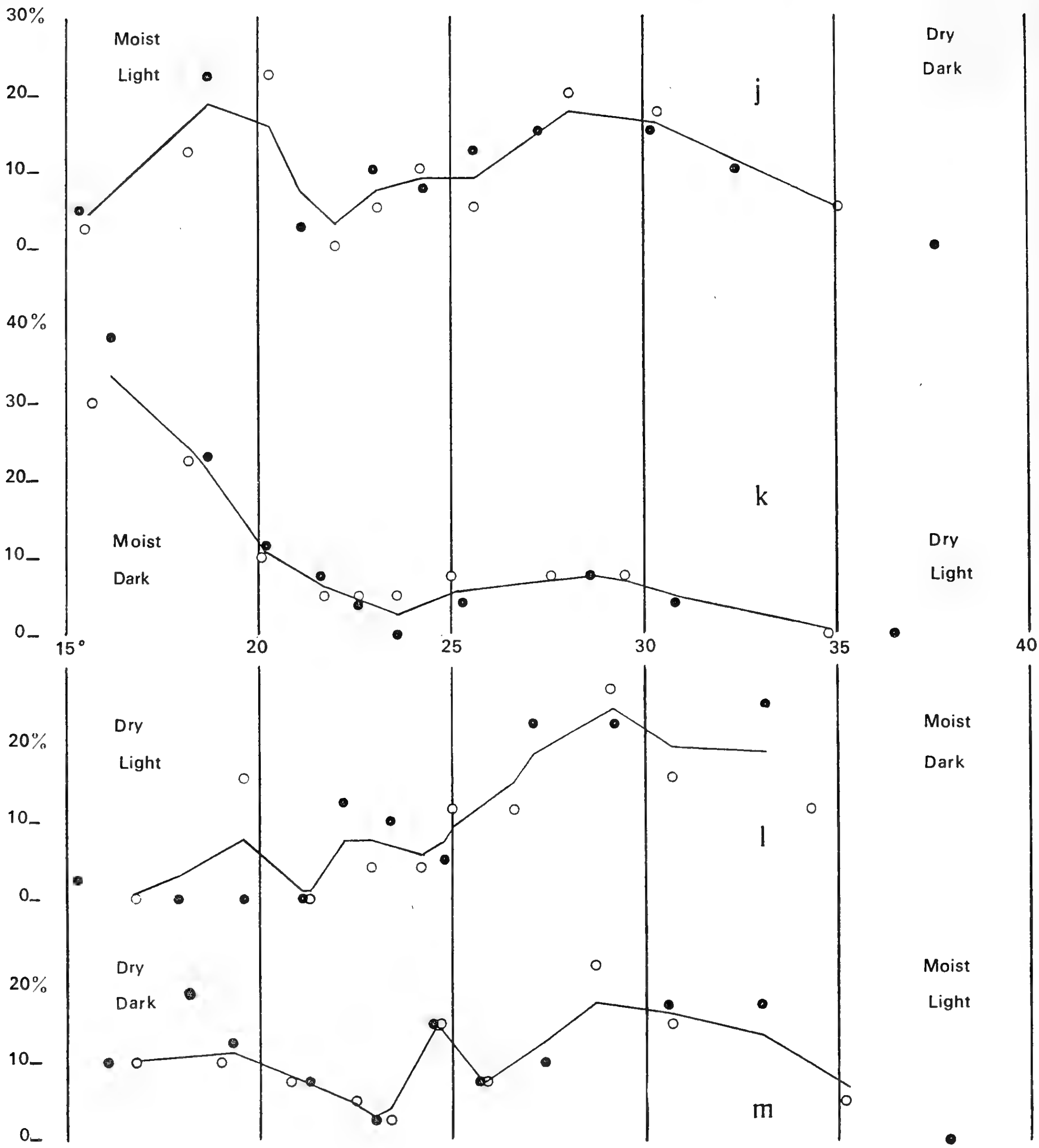


Diagram 29 j–m. *Harpalus punctatulus*. Universal gradient apparatus. Experiment 112 (p. 99). See Diagram 25 and p. 175.

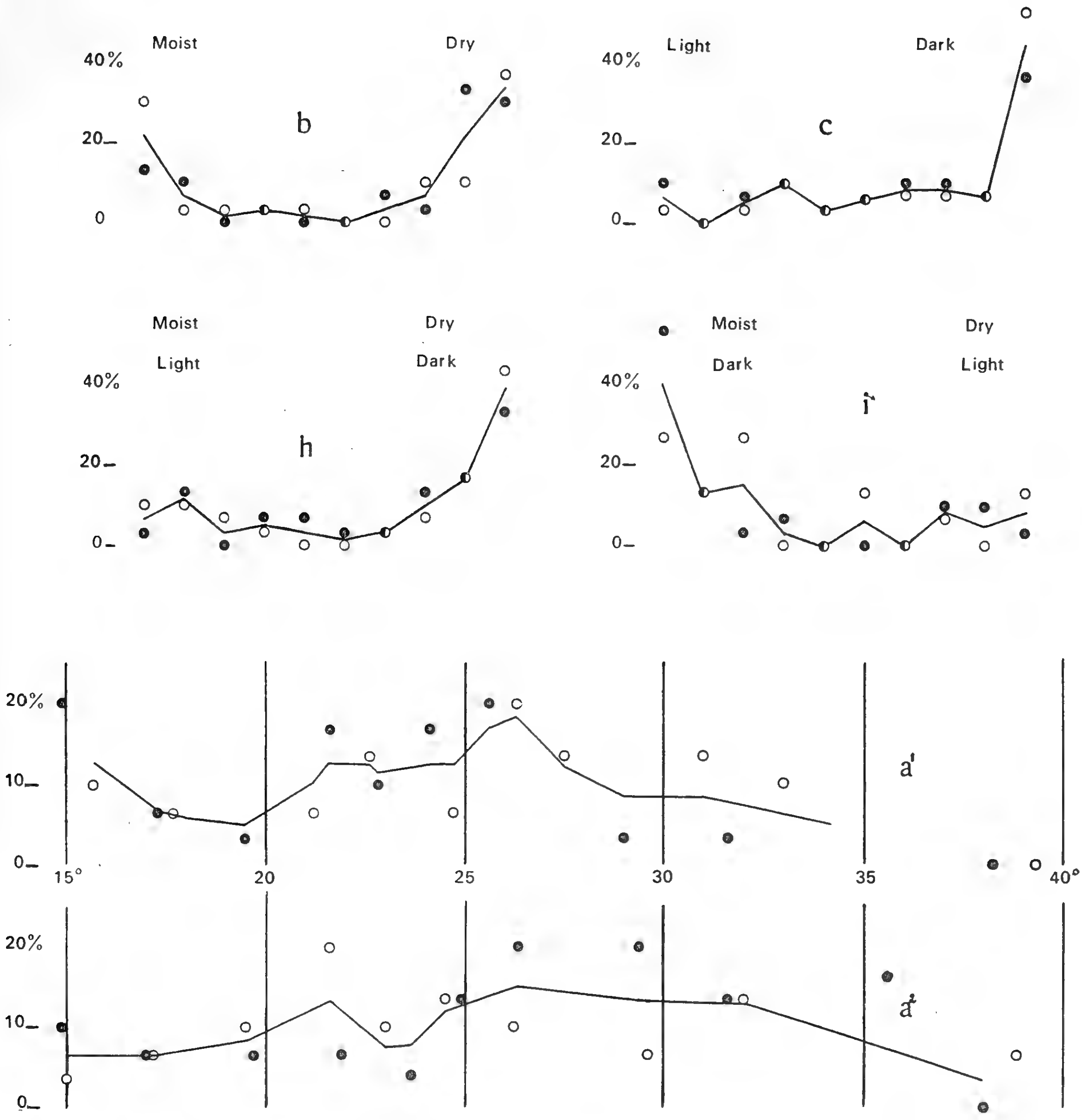


Diagram 30 a–c, h–i. *Harpalus rubripes*. Universal gradient apparatus. Experiment 113 (p. 99). See Diagram 25 and p. 176.

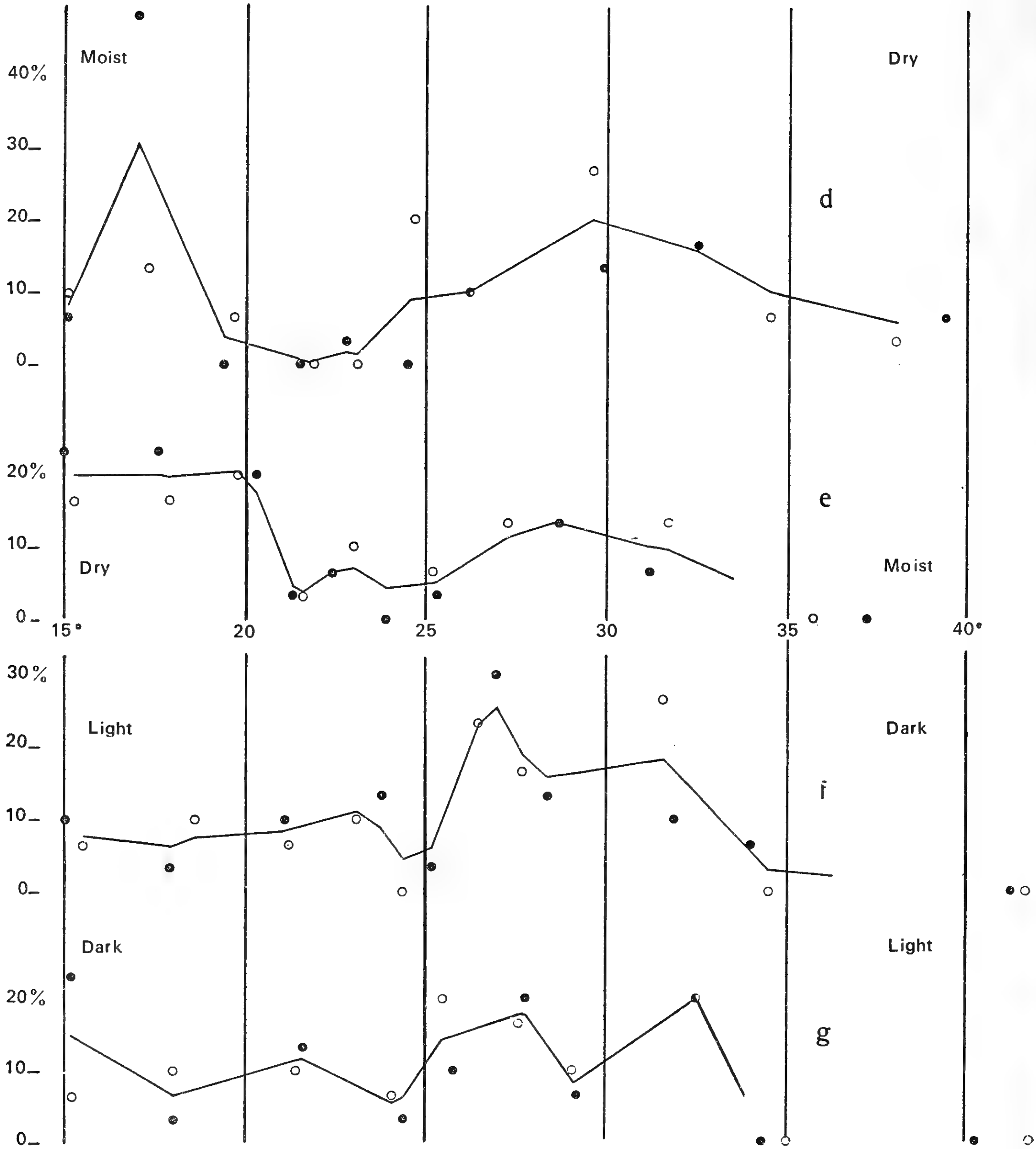


Diagram 30 d–g. *Harpalus rubripes*. Universal gradient apparatus. Experiment 113 (p. 99). See Diagram 25 and p. 176.

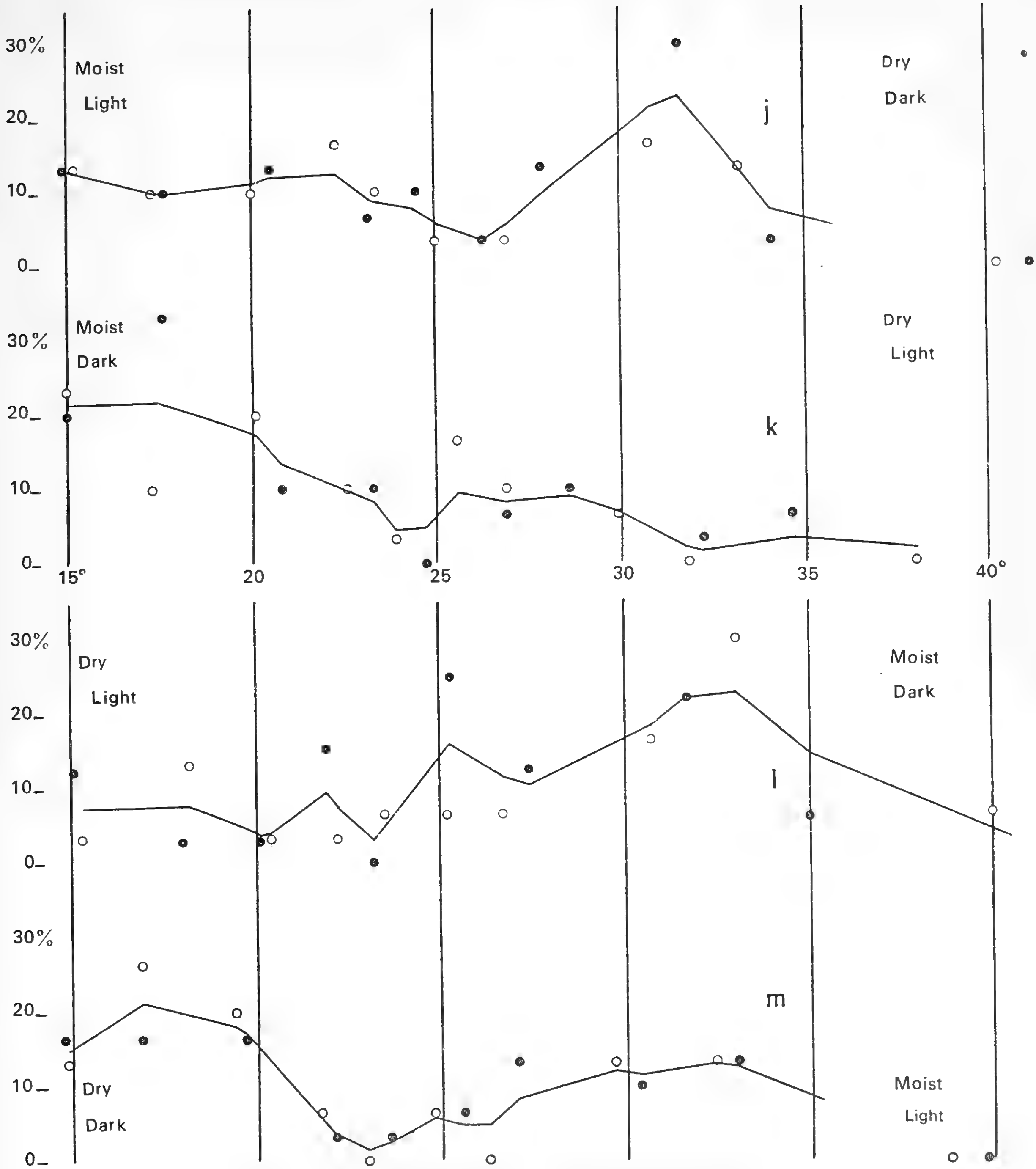


Diagram 30 j–m. *Harpalus rubripes*. Universal gradient apparatus. Experiment 113 (p. 99). See Diagram 25 and p. 176.

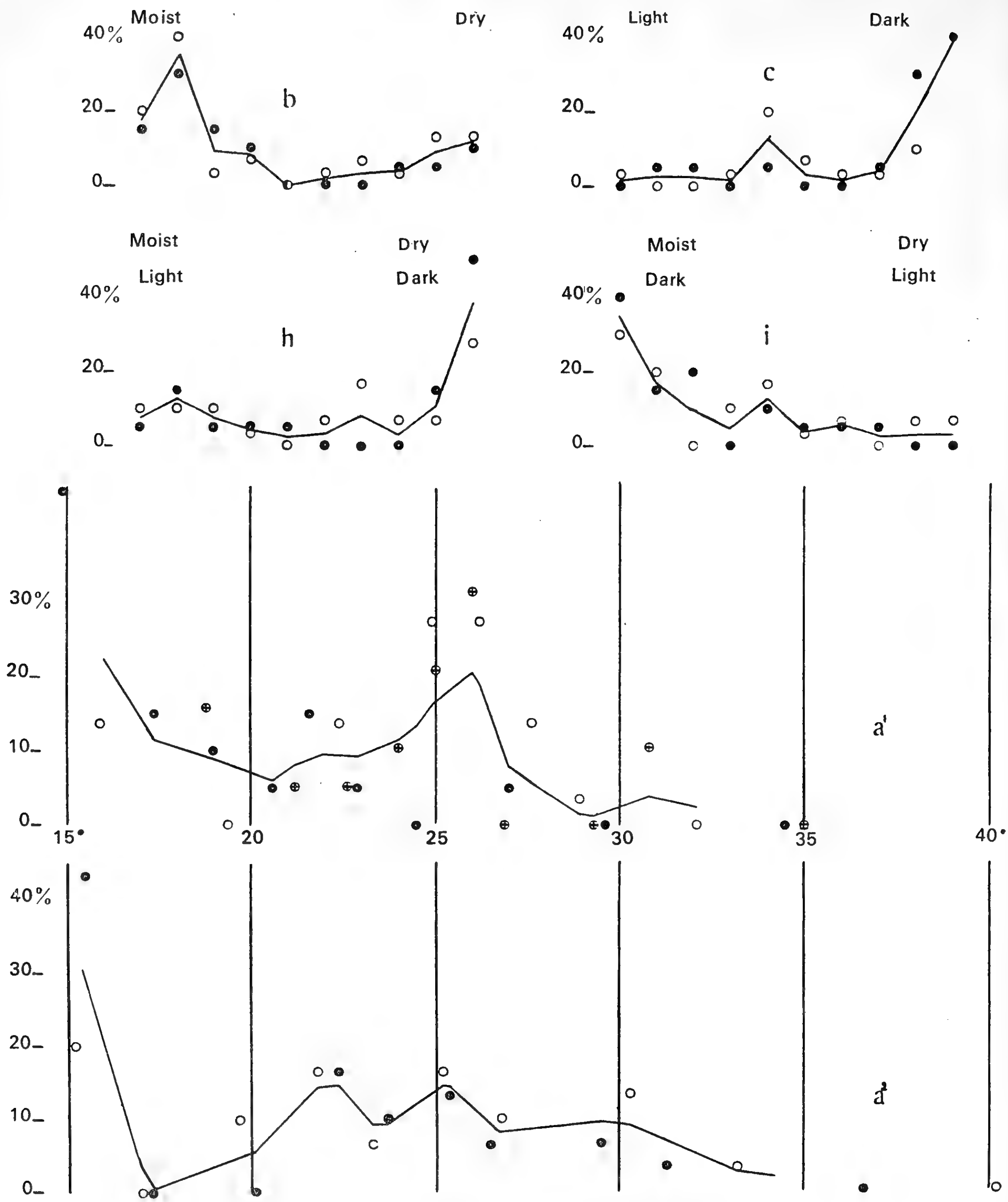


Diagram 31 a–c, h–i. *Harpalus rupicola*. Universal gradient apparatus. Experiment 114 (p. 100). See Diagram 25 and p. 176.

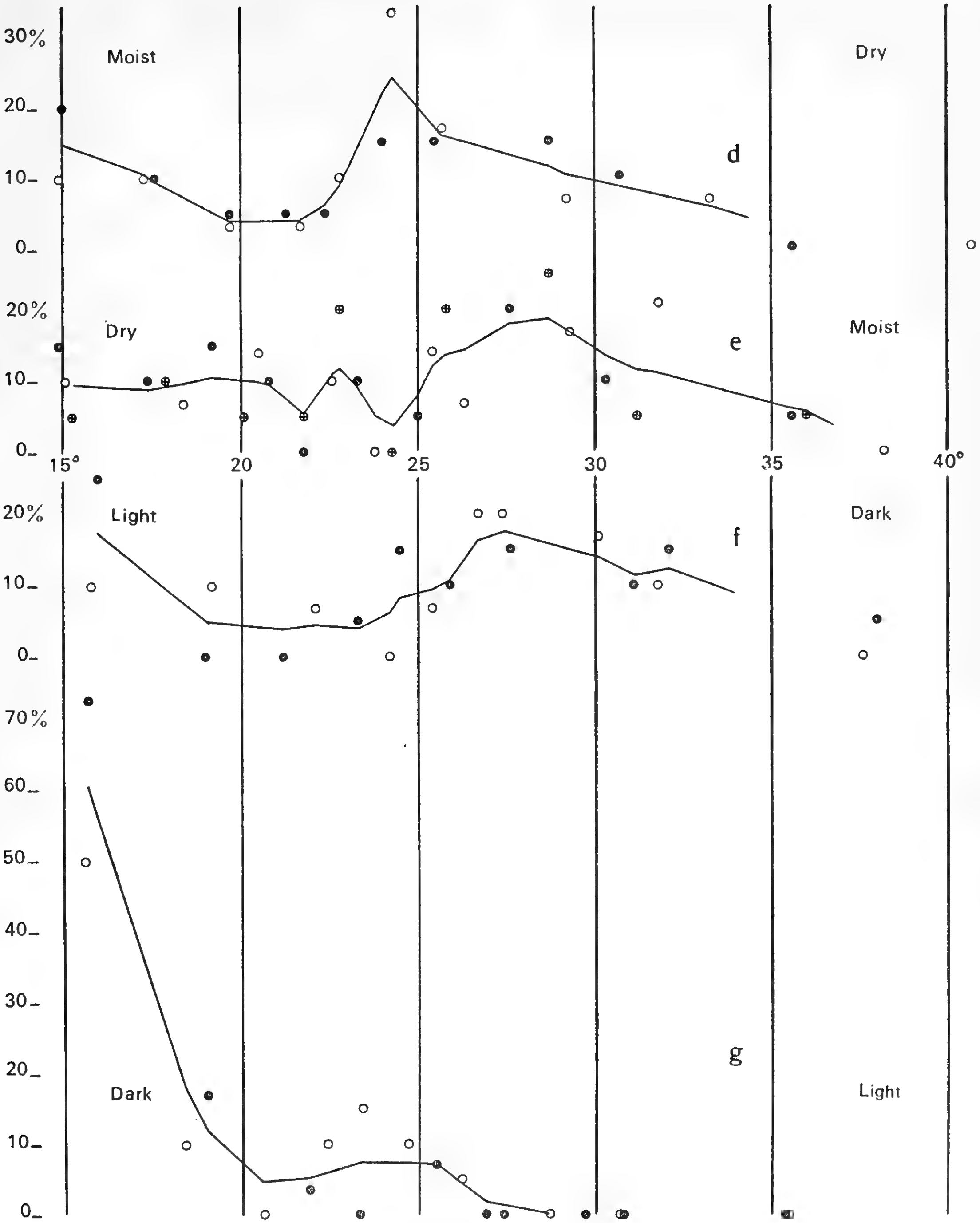


Diagram 31 d–g. *Harpalus rupicola*. Universal gradient apparatus. Experiment 114 (p. 100). See Diagram 25 and p. 176.

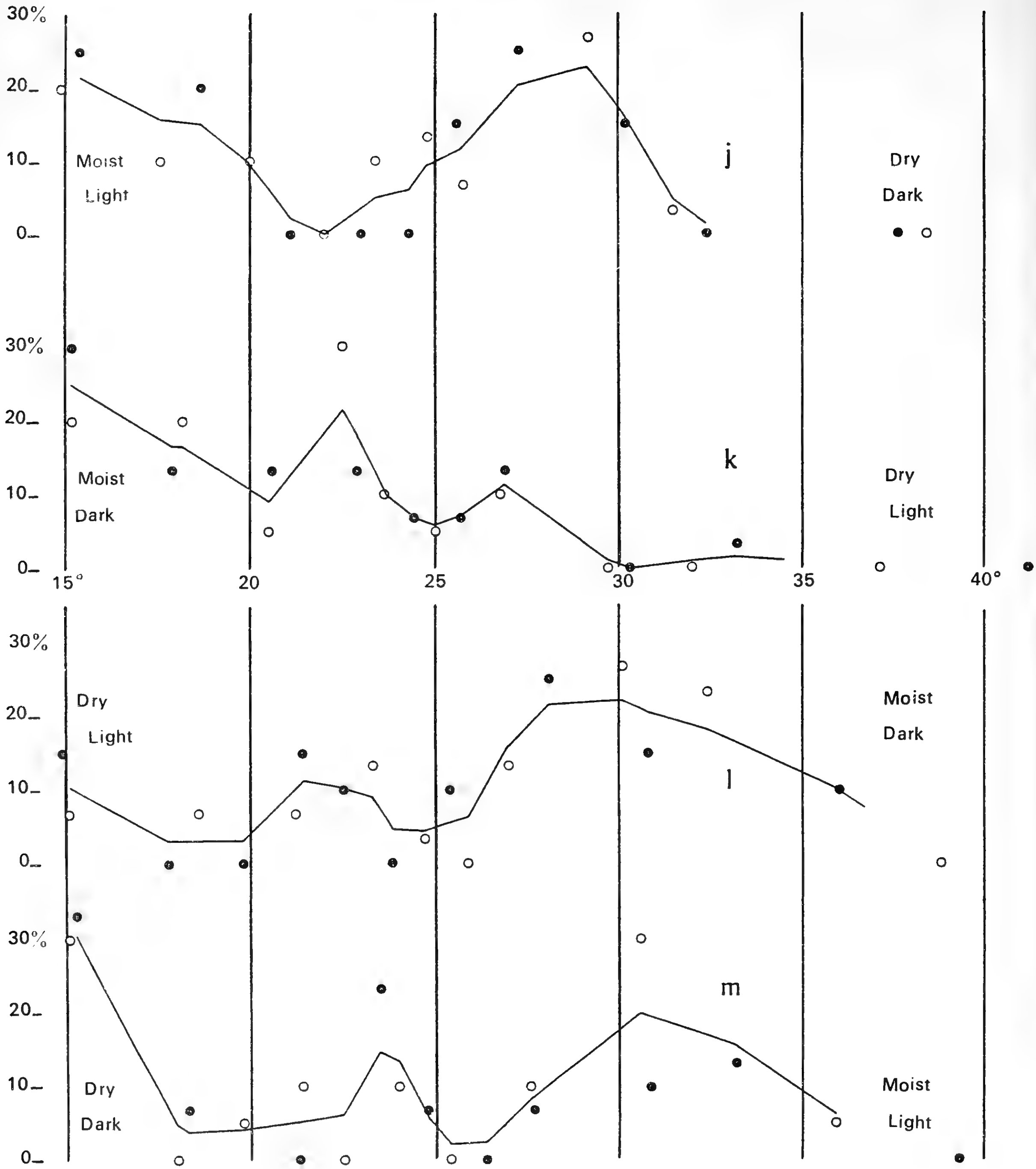


Diagram 31 j–m. *Harpalus rupicola*. Universal gradient apparatus. Experiment 114 (p. 100). See Diagram 25 and p. 176.

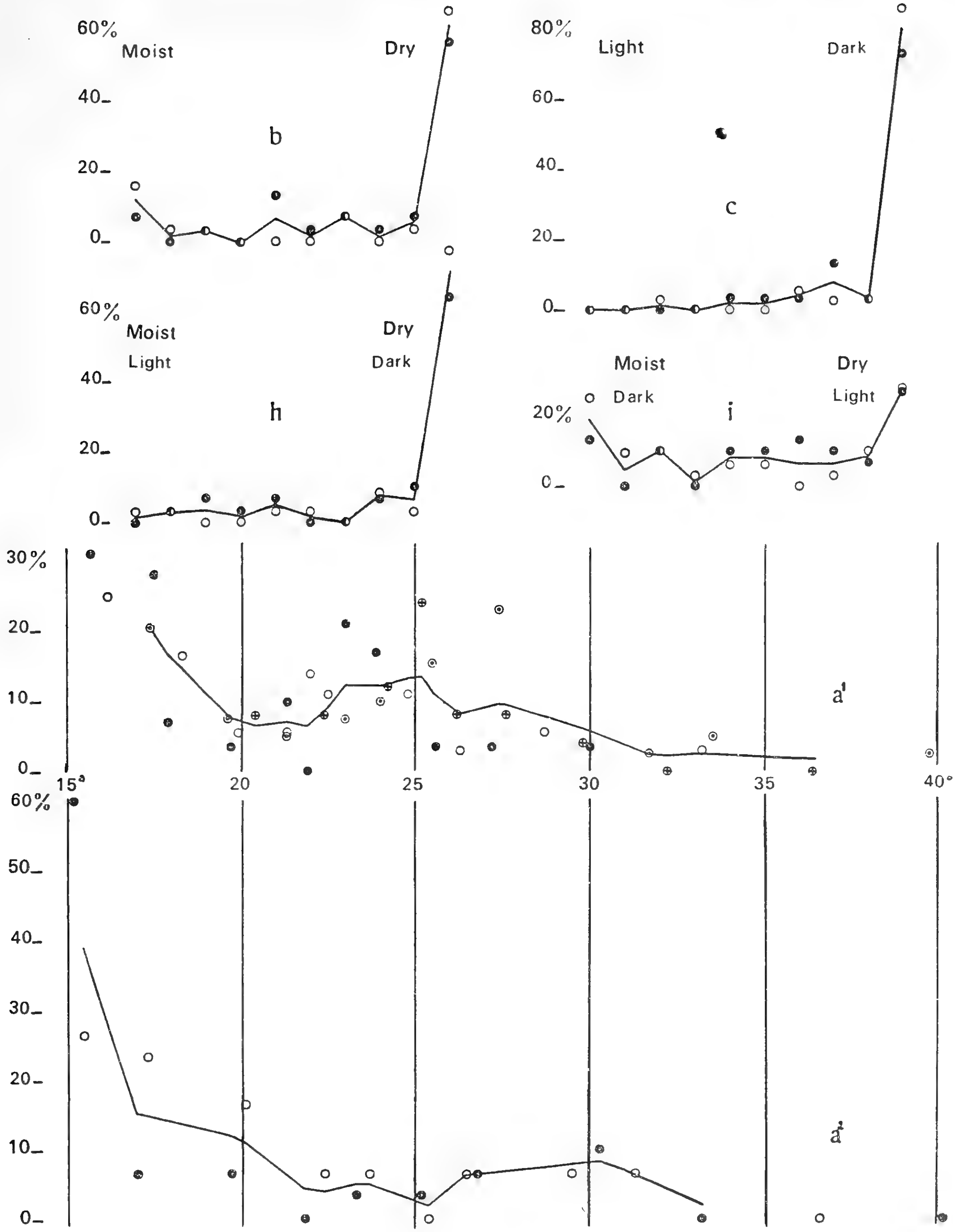


Diagram 32 a–c, h–i. *Harpalus seladon*. Universal gradient apparatus. Experiment 115 (p. 100). See Diagram 25 and p. 176.

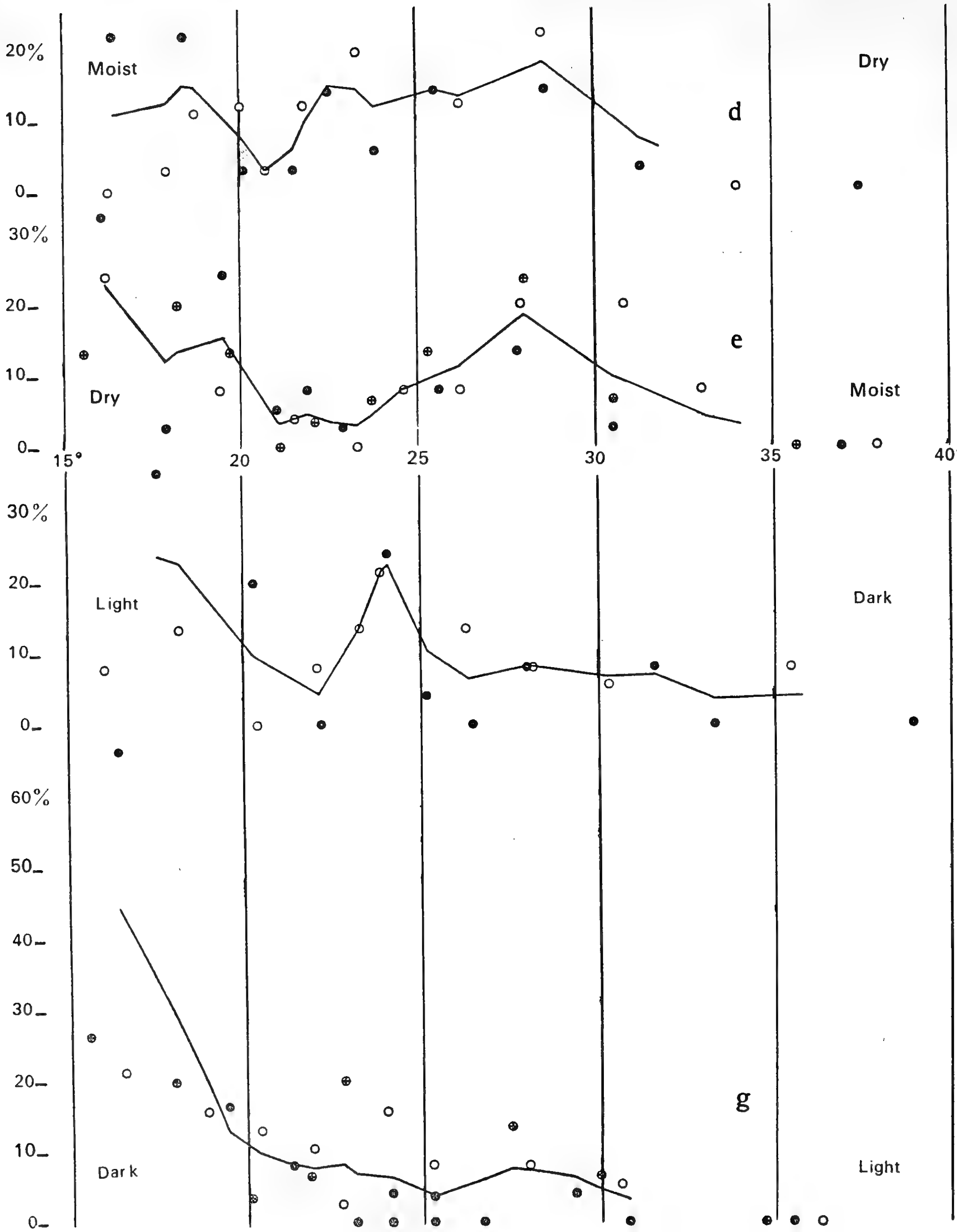


Diagram 32 d–g. *Harpalus seladon*. Universal gradient apparatus. Experiment 115 (p. 100). See Diagram 25 and p. 176.

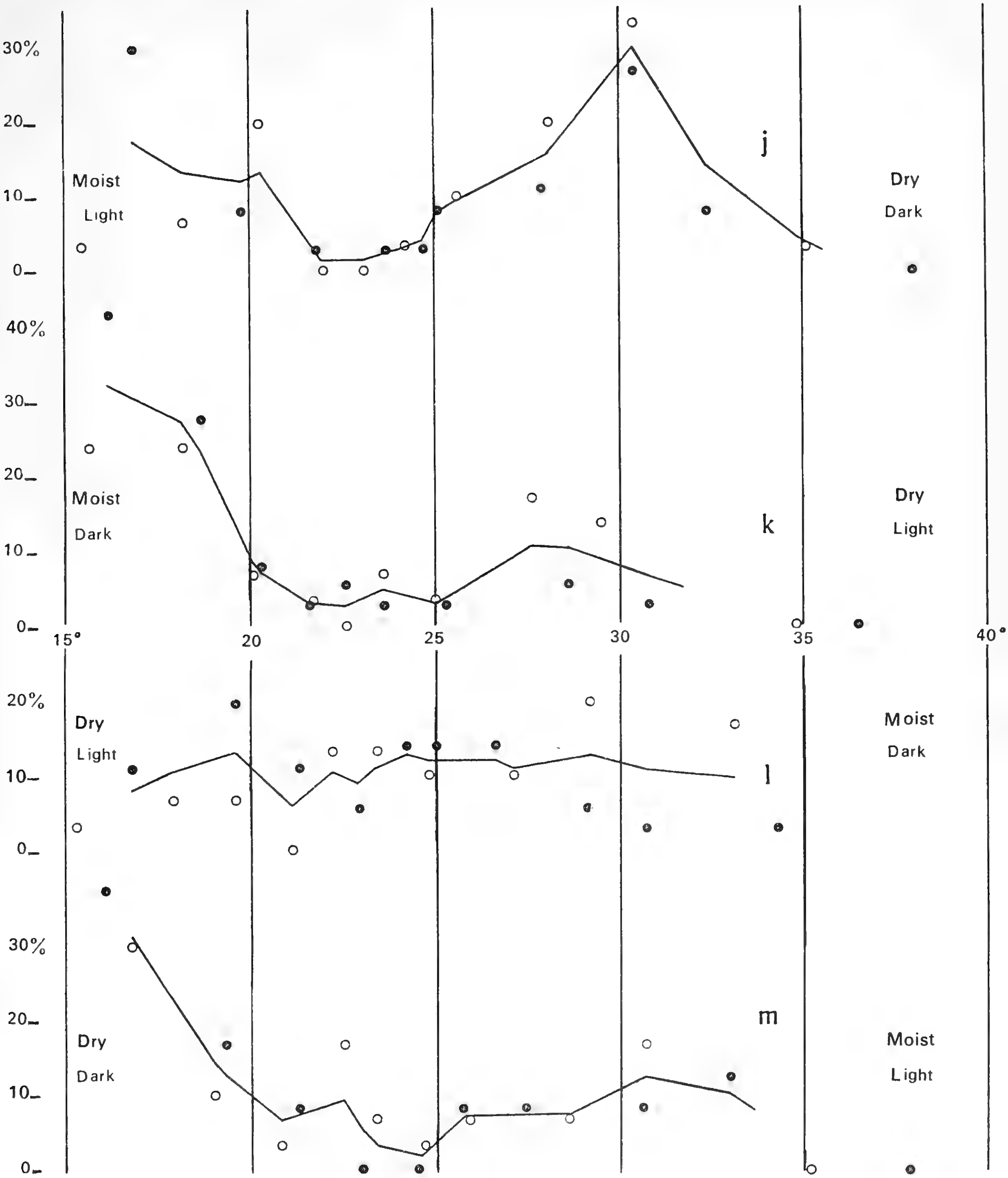


 Diagram 32 j–m. *Harpalus seladon*. Universal gradient apparatus. Experiment 115 (p. 101). See Diagram 25 and p. 176.

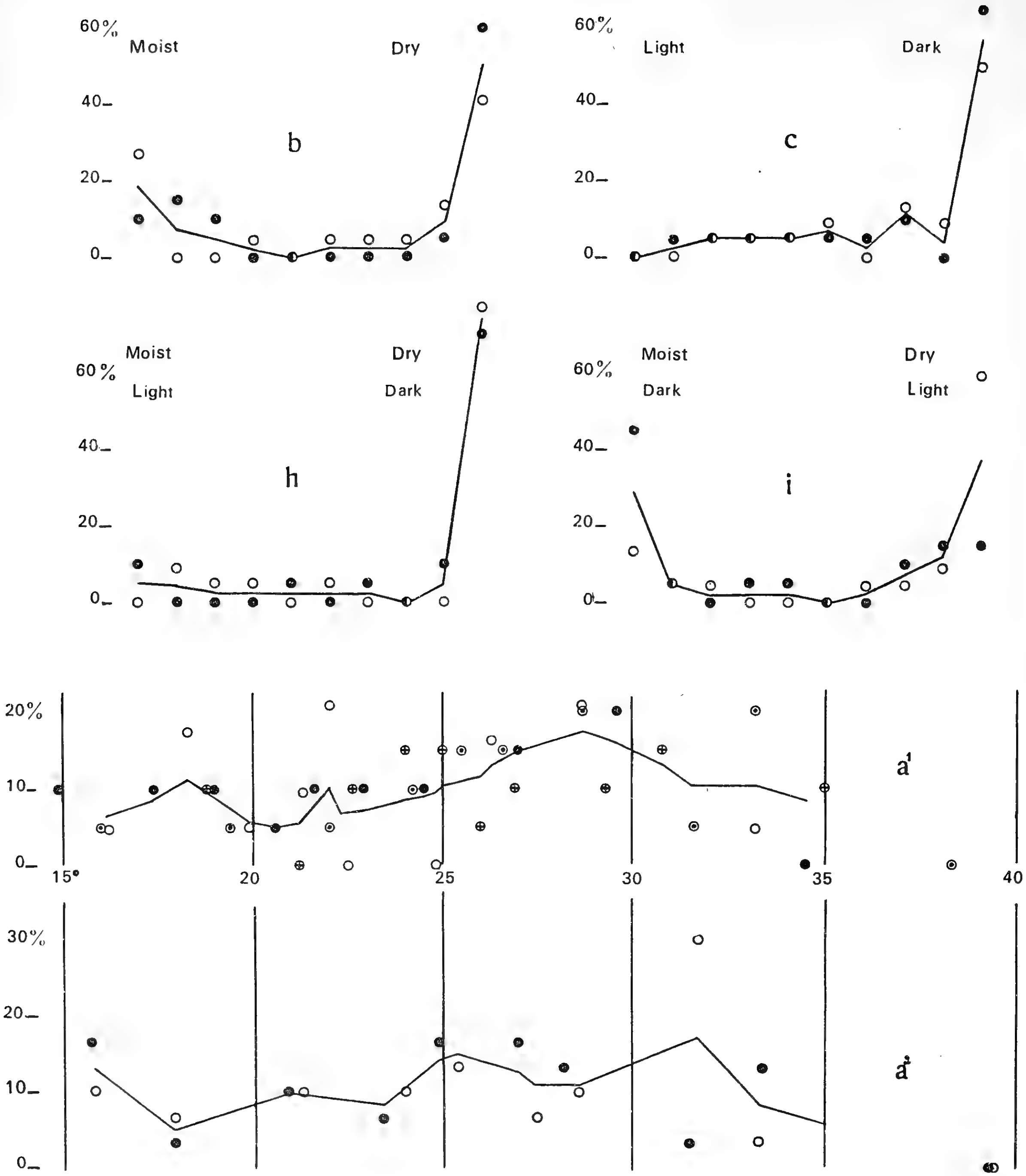


Diagram 33 a–c, h–i. *Harpalus serripes*. Universal gradient apparatus. Experiment 116 (p. 101). See Diagram 25 and p. 174.

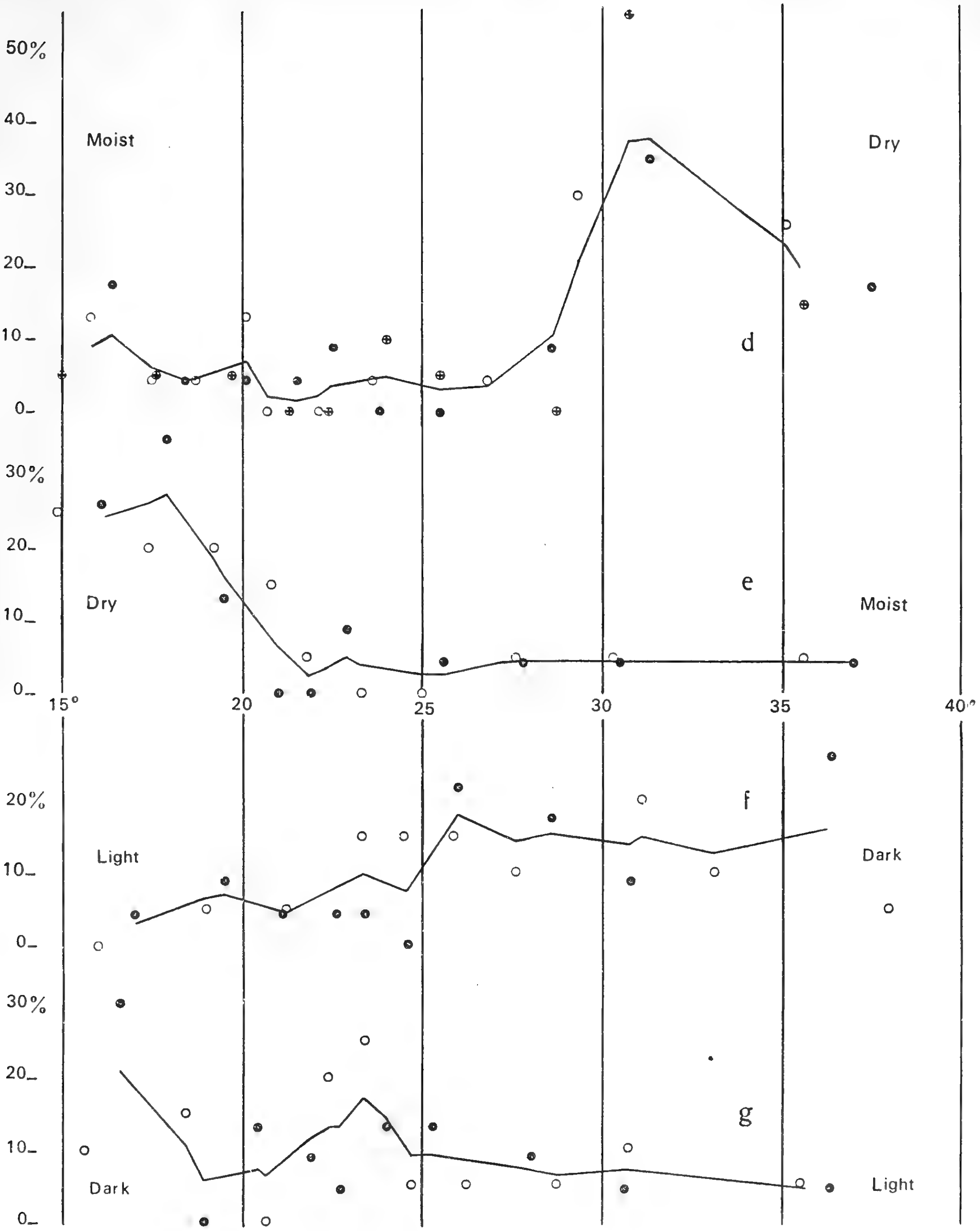


Diagram 33 d–g. *Harpalus serripes*. Universal gradient apparatus. Experiment 116 (p. 101). See Diagram 25 and p. 174.

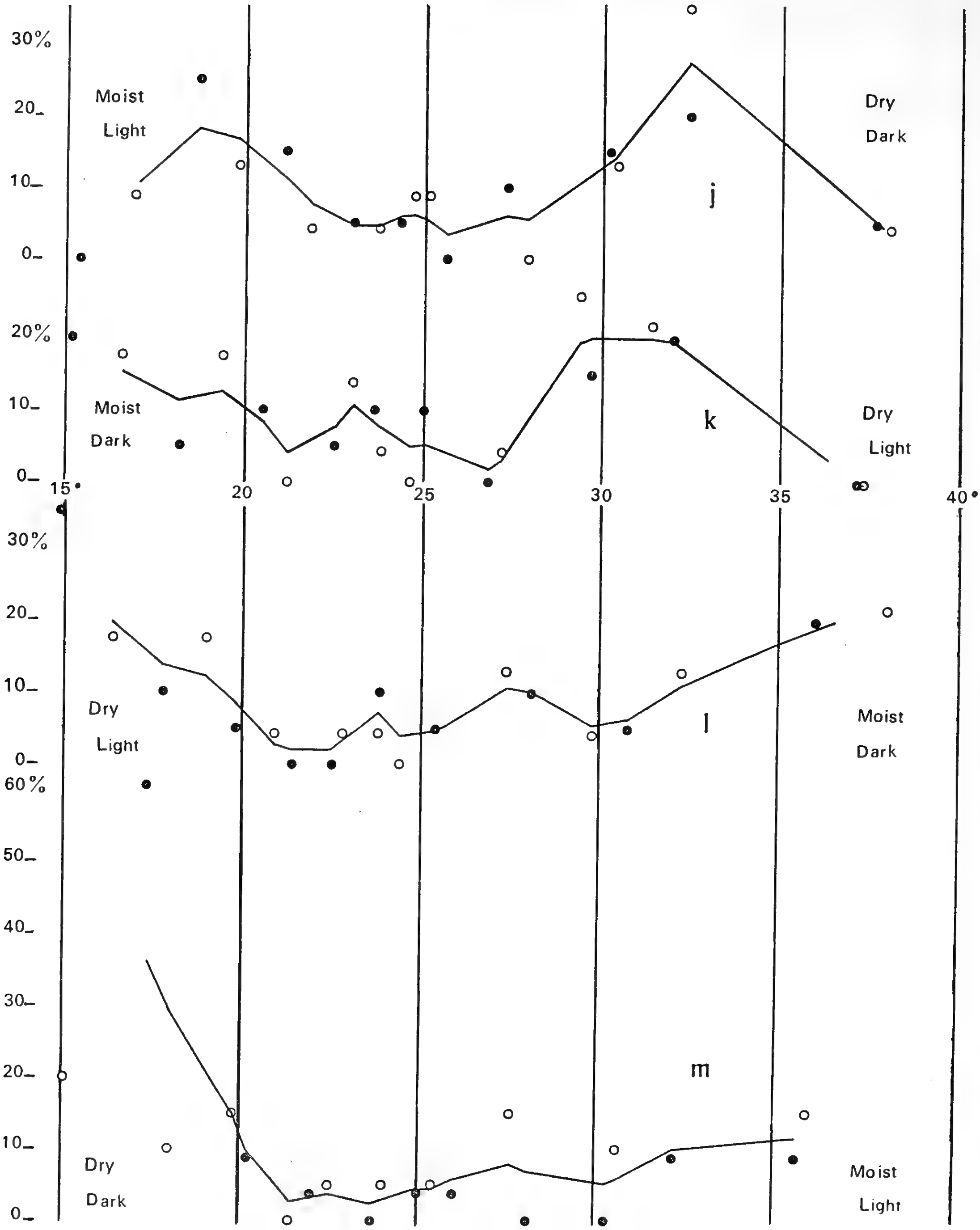


Diagram 33 j–m. *Harpalus serripes*. Universal gradient apparatus. Experiment 116 (p. 101). See Diagram 25 and p. 174.

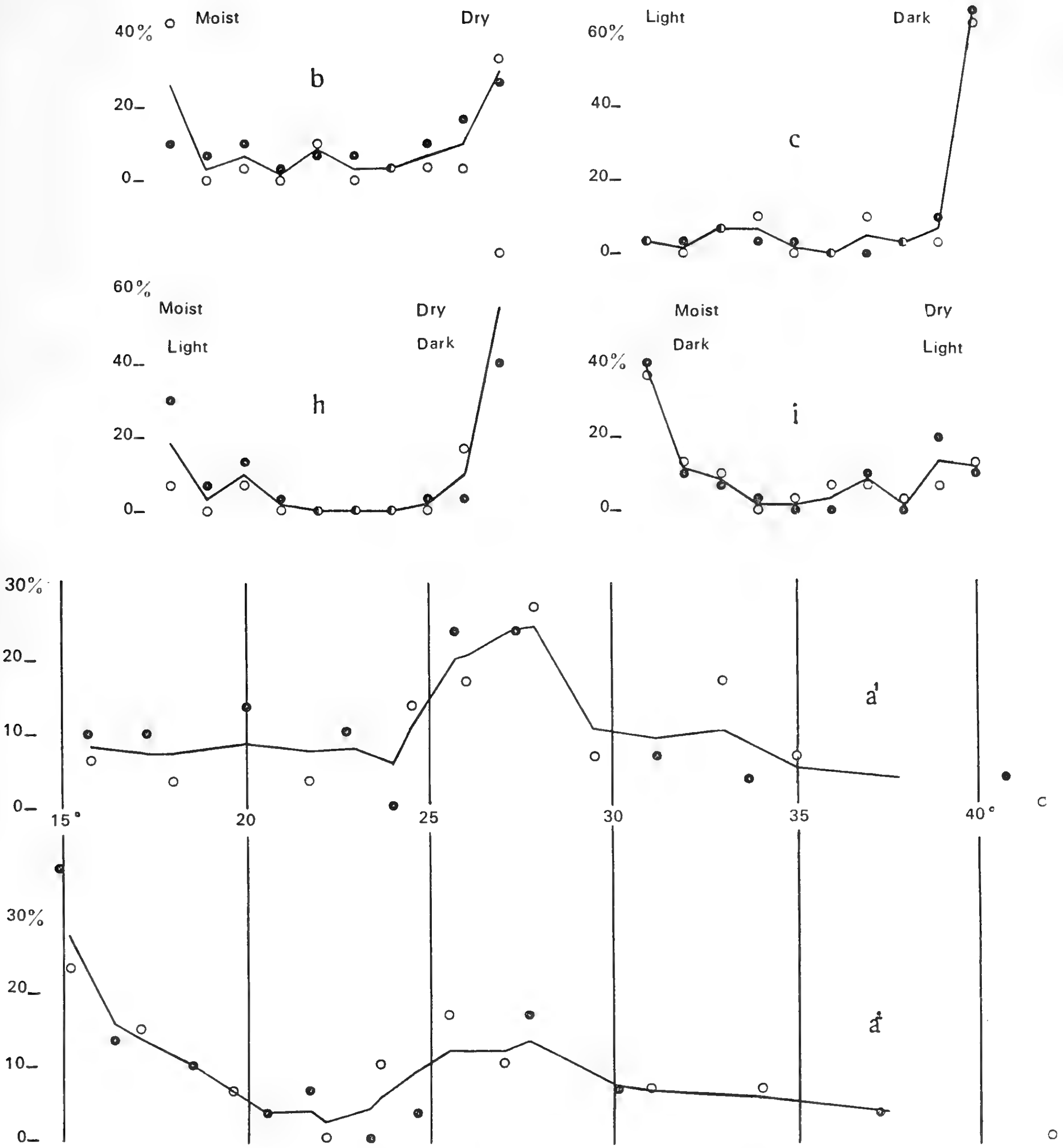


 Diagram 34 a–c, h–i. *Harpalus smaragdinus*. Universal gradient apparatus. Experiment 117 (p. 101). See Diagram 25 and p. 176.

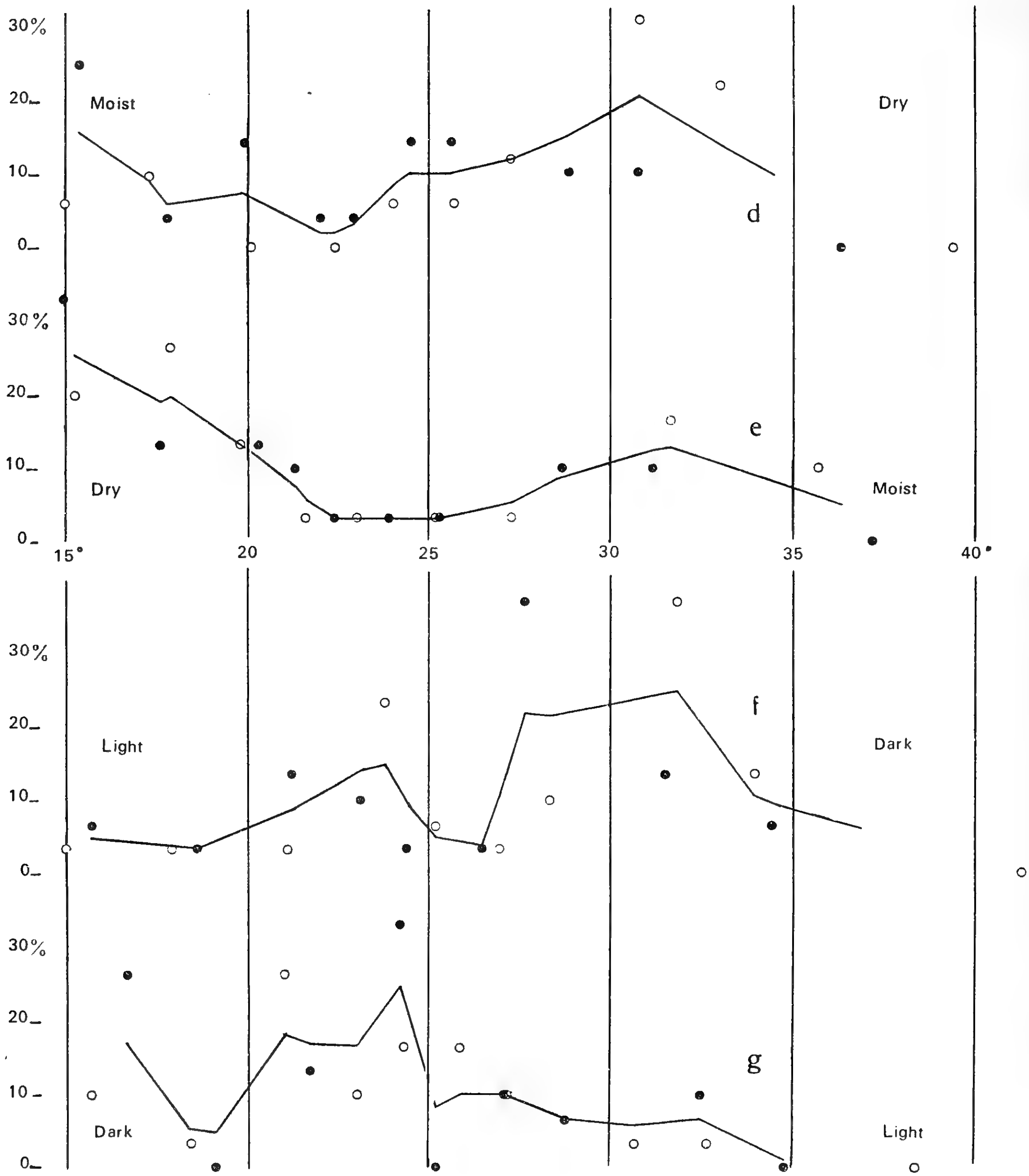


Diagram 34 d–g. *Harpalus smaragdinus*. Universal gradient apparatus. Experiment 117 (p. 102). See Diagram 25 and p. 176.

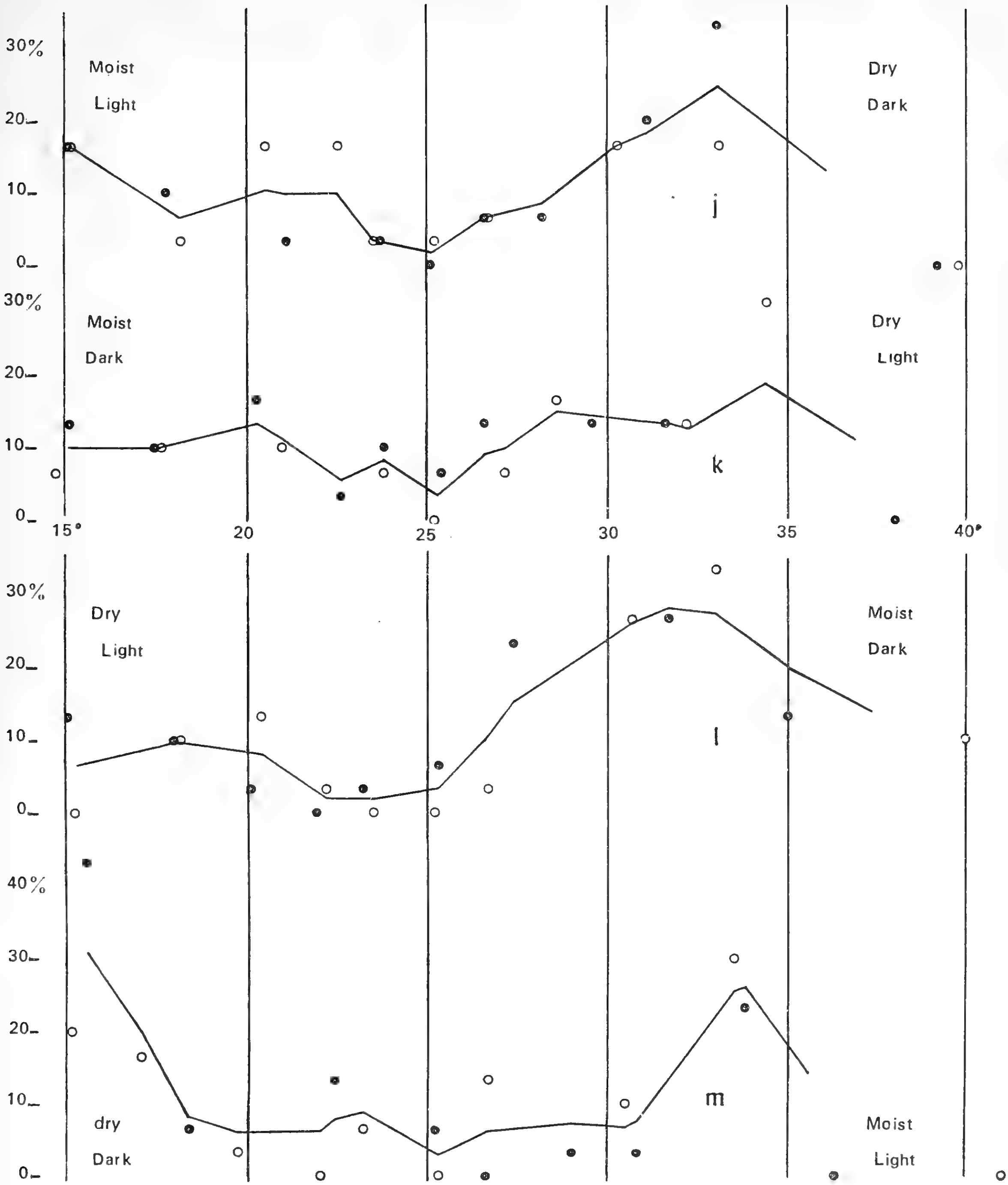


Diagram 34 j–m. *Harpalus smaragdinus*. Universal gradient apparatus. Experiment 117 (p. 102). See Diagram 25 and p. 176.

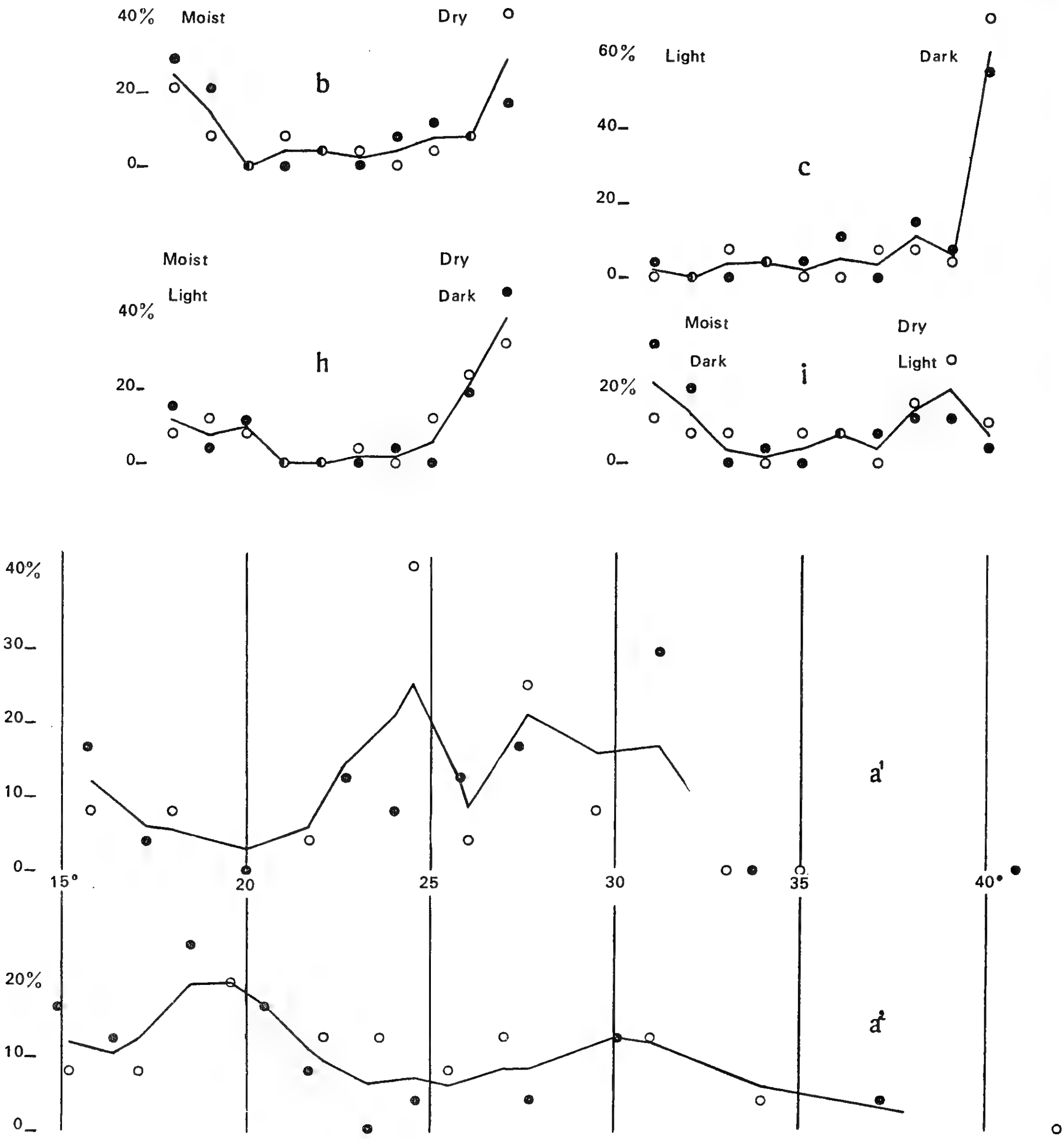


Diagram 35 a–c, h–i. *Harpalus tardus*. Universal gradient apparatus. Experiment 118 (p. 102). See Diagram 25 and p. 176.

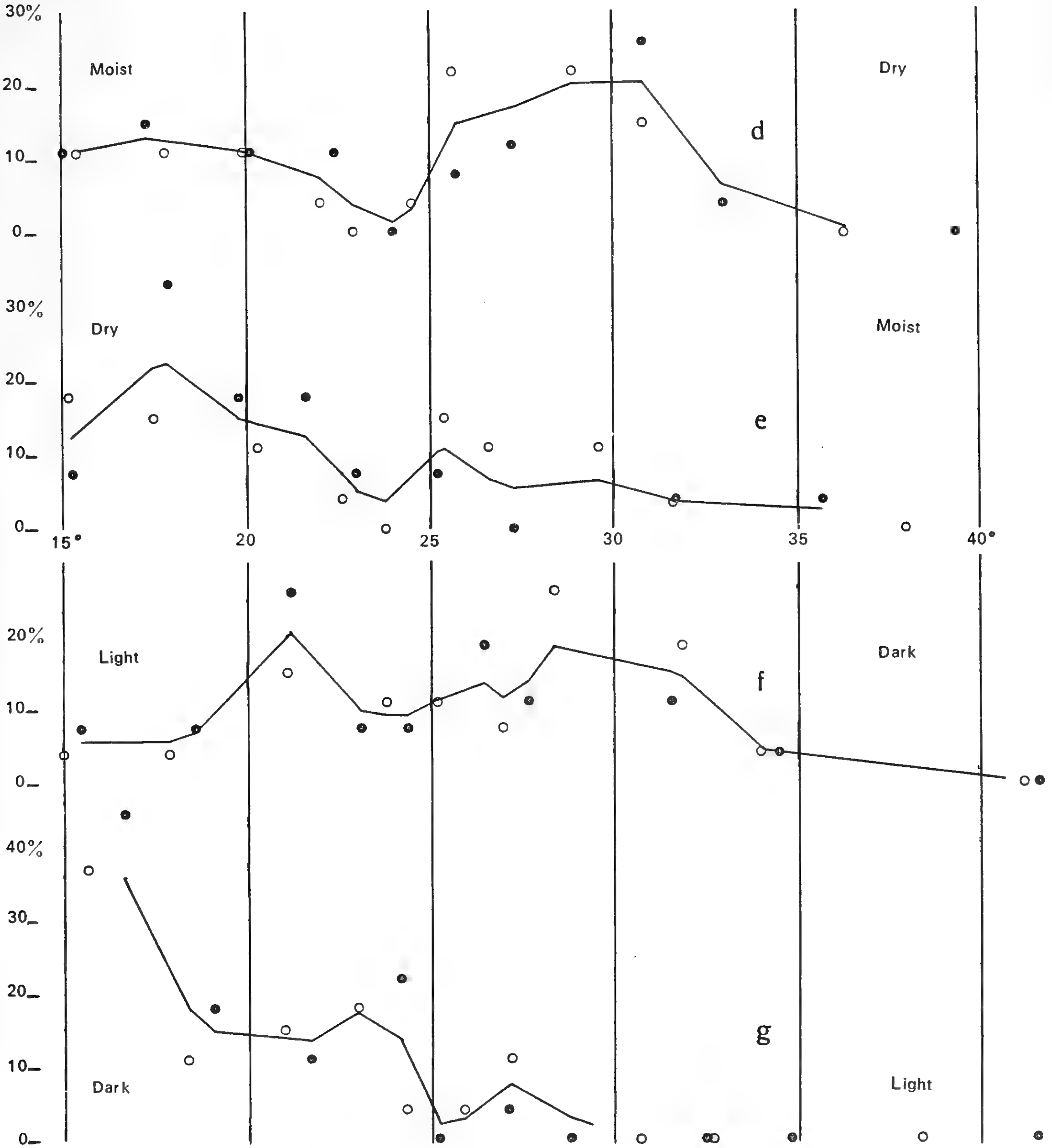
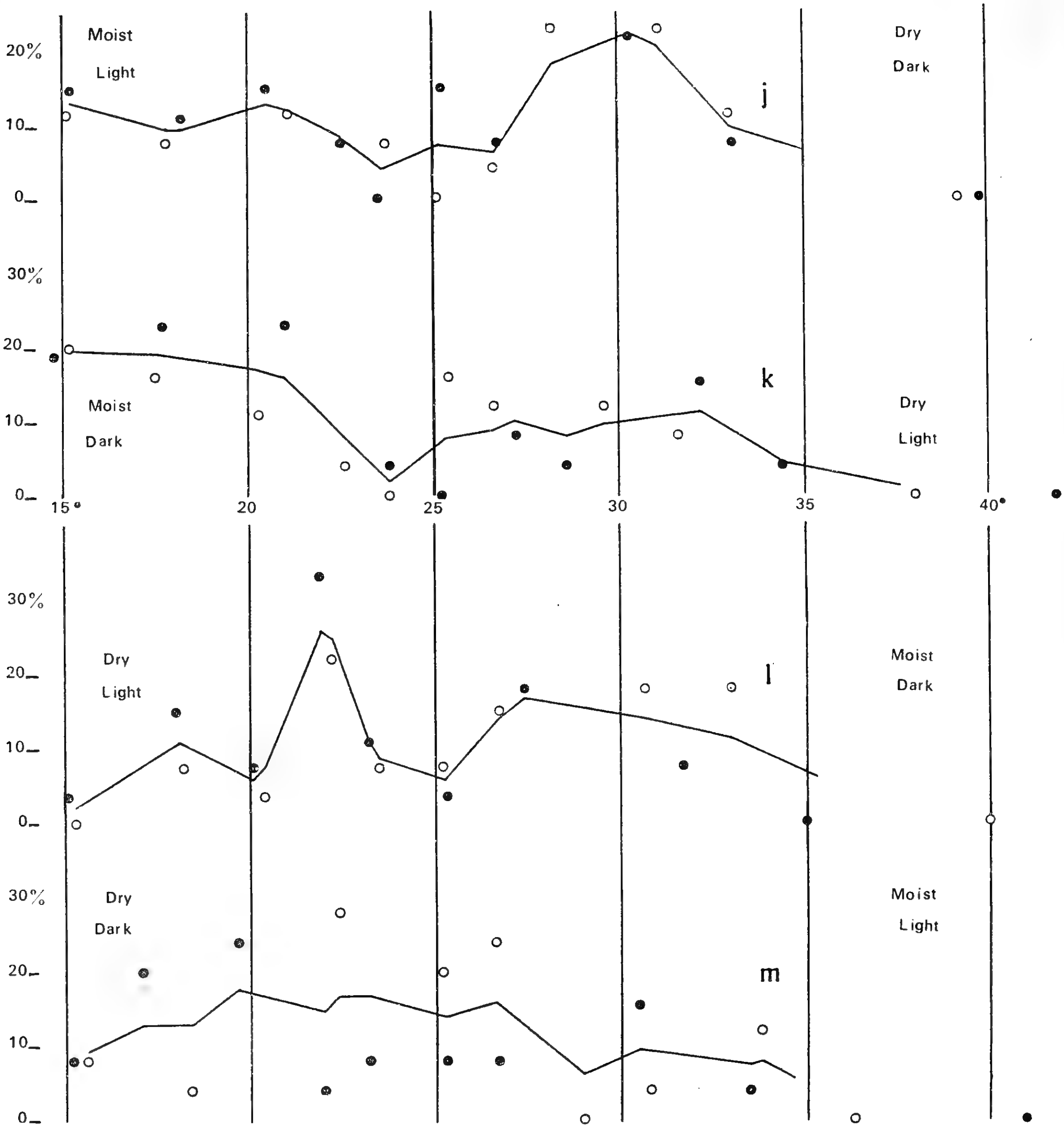


Diagram 35 d–g. *Harpalus tardus*. Universal gradient apparatus. Experiment 118 (p. 102). See Diagram 25 and p. 176.



173 Diagram 35 j–m. *Harpalus tardus*. Universal gradient apparatus. Experiment 118 (p. 102). See Diagram 25 and p. 176.

experiments was the most *thermophilous* of the 15 species tested (but only 8th in xerophilous ranking: Table 7); and on the other hand *H. serripes*, which was the most *xerophilous* species after *H. hirtipes* (only 10th in thermophilous ranking).

This difference is already evident in the one-factor experiments (Diagrams 27 a–c, 33 a–c) in the universal gradient apparatus. The temperature
175 preferendum in *azureus* is far more pronounced and lies (especially with dry sawdust (a^1)) about 3° higher. On the other hand *serripes* shows a stronger attraction to the dry end of the apparatus (b). Besides, it is much more heliophobous (c).

In the two-factor experiments (with the temperature factor) the difference becomes pronounced. If the temperature and humidity are similarly directed (d) the beetles behave almost identically with a very sharp maximum at 30–31°C. If the same factors are differently directed (e), *serripes* at once moves to the cold end, whereas *azureus* is remarkably undecided. In one of the two experiments most of the animals congregated in the colder (drier) half, but in the other experiment, in the warmer (moister) half of the apparatus, and the mean plot has two marked peaks. —Likewise the light factor (f, g) produced much stronger variation of the temperature preferendum in *serripes* than in *azureus*.

The three-factor experiments (j–m) are still more informative. *H. azureus*, in all combinations, retains a distinct maximum at about 32°C, but *serripes* does so only if the humidity factor is similarly directed with the temperature (j, k). If not, it moves mostly to the cold end, even if the light factor, against which it otherwise reacts very strongly, is differently directed.

Certainly the results of the experiments with *azureus–serripes* also reveal incongruities that cannot be explained by insufficient observation material. Examples are the secondary maximum of *serripes* at 20°C with all factors similarly directed (33j), or the question, why a different direction of the humidity factor alone (e) causes a steeper decline in the temperature preferendum than both humidity and light together (m).

However, the general tendency in both these species is quite clear. The universal gradient apparatus experiments greatly strengthen the earlier conclusions that for *azureus* the temperature factor is decisive and for *serripes* the humidity factor.

A counterpart of the constantly high temperature preferendum of *azureus* was not found among the remaining species tested in the universal gradient apparatus. *H. punctatulus*, which comes after *azureus* (and *puncticeps*) in the ranking list given in Table 7, shows very irregular responses (Diagram 29), which is certainly related with the peculiar labile humidity preferendum of this species (pp. 57 ff.).

H. anxius belongs to the *serripes* type. But in the latter species the temperature factor evidently has a much stronger effect. The experiments with

differently directed temperature and humidity have especially to be compared
176 (Diagrams 26e, 33e). In the earlier ranking order of thermophily (Table 7), *anxius* certainly has too low a place, chiefly because of its low "lower response point" ("point b").

In contrast with the species discussed so far, which show a sharply delimited preferendum zone in most of the temperature gradient apparatus experiments, *H. aeneus* (Diagram 25) may be singled out. It reacts strongly and consistently to the light factor (c, f, g, etc.), and to some extent also to variations in humidity. But the temperature and different combinations of factors with it, especially in the two-factor experiments (d–g), elicit very diffused responses. It is highly characteristic that a strongly pronounced maximum appears only in the three-factor experiment in which all three factors are similarly directed (Diagram 25j). *It is characteristic of an eurytopic and at the same time widely distributed species that its temperature preferendum is not only low but is also less fixed and consequently can easily be displaced by other factors.* —An exactly similar characteristic is shown by *H. seladon* (Diagram 32). In the similarly widely distributed but somewhat less eurytopic (xerophilous) *H. tardus* (Diagram 35) a deviation is discernible only to the extent that the inclination for dryness is somewhat more established (d, e, l).

A median position is occupied by *H. rubripes* (Diagram 30) and *H. smaragdinus* (Diagram 34), which have almost identical Fennoscandian distribution (Swedish northern limit in Northern Upl) and are also very closely related ecologically (occurring on more or less dry sandy and gravely soil). Their behavior in the universal gradient apparatus is largely identical. Their temperature preferendum is much more fixed than in *aeneus, seladon*, and *tardus* (cf. especially the two-factor experiments; they are "southern" species). But the humidity factor, much as in *tardus*, shows a more distinct influence throughout (they are markedly more xerophilous).

The two remaining species, *H. melleti* and *H. rupicola*, are distinct in several ways. The earlier one-factor experiments showed (see ranking list in Table 7, p. 137) that they are neither distinctly thermophilous nor xerophilous. Yet both species occur in the extreme south, *rupicola* being actually confined to Öld and Gtl. The universal gradient apparatus experiments (Diagrams 28, 31) confirm that their temperature preferendum is not only comparatively low but is also easily displaced by other factors, for instance light (g). *H. rupicola*
177 is found to be at least as little xerophilous as *seladon* (Diagram 31e, k–m), whereas *melleti* has somewhat higher requirements in this respect.

Those factors, which are responsible for the restricted southern distribution of *melleti* and *rupicola*, apparently were not revealed by the universal gradient apparatus experiments. However, an indication is perhaps provided by the earlier finding of the strikingly high "lower response point" with regard to temperature in both these species (Diagram 20; Table 7), i.e. as in *azureus* and *punctatulus*, the short duration of their continuous annual activity period.

At present it is not known whether a particular thermal sensitivity of the larvae is decisive, but it seems less probable, since this stage is passed through in both cases in midsummer.

The conclusions drawn from the experiments with the universal gradient apparatus may be summarized as follows:

1. If one of the factors studied exercises an especially strong effect it is possible to determine it. For example: temperature (*azureus*), humidity (*serripes*).

2. Species that are widely distributed and at the same time eurytopic (*aeneus, seladon, tardus*), have weakly fixed temperature and humidity preferenda, so that the distribution of the animals in the apparatus is determined mainly by the light factor. A factor that certainly has no more than a subordinate role in the choice of biotope in the case of more or less subterranean soil animals and which probably has no role at all in the geographical distribution (with regard to area limits). According to responses, such geographically and ecologically ubiquists can be designated "*euryphysic*" ("euryphys") species in contrast to the more or less "*stenophysic*" ("stenophys") species.

3. The examples of *melleti* and *rupicola* nevertheless show that restricted distribution (in our case markedly southern) is not always related to the requirements for life demonstrated by the preferenda experiments. Probably, distribution is yet influenced by temperature. A conformity exists in the results obtained with *Agonum dorsale* and *Brachynus* (p. 61), according to which "the lower response point," i.e. the resistance to low temperatures, may have a greater role than the position and magnitude of the thermal preferendum.

Characteristics of Limestone Rock and Limestone Gravel

On the basis of the experiments carried out with the presumed "limestone species" the chemical characteristics of $CaCO_3$ appear to have no influence
178 on the animals concerned, but these animals are characterized by pronounced requirements of heat or dryness (or both).

In the following experimental study of limestone rock and limestone gravel it was especially important to determine the thermal and hygric characteristics thereof.

The *temperature* experiments were first carried out on a small scale as laboratory studies. A series of day experiments with readings every hour were run on the roof of the school in Djursholm from July 1, 1945 (5 a.m.) through July 2 (6 a.m.), with rock and gravel (Experiments 153, 154, p. 110).

The two squarish pieces of *rock* were about 15 cm^2 in area and about 3 cm thick. They comprised Gotland limestone (weight by volume 2.629) and fine-grained Uppland granite (weight by volume 2.646). These rocks had a very similar gray color (Thurmann, 1849, pp. 109–111, already stated that color

has an important role in the absorption of heat by rock). Thermometers were placed underneath the rocks on aluminum foil, and this face was isolated with thick saddler felt.

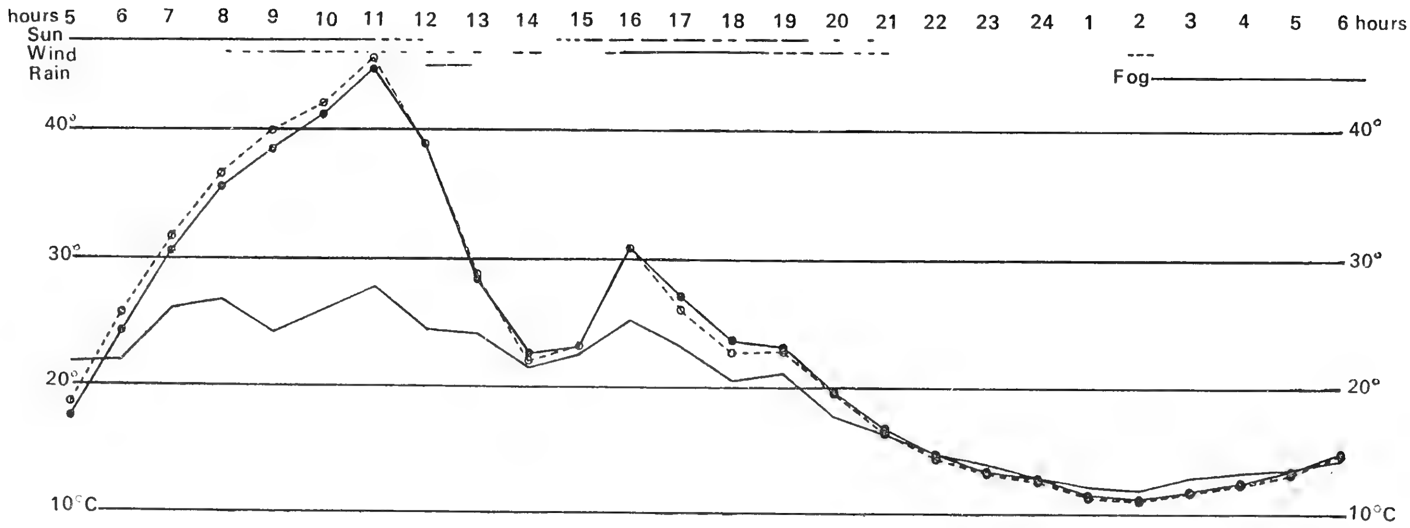
The *gravel* consisted of the types described above (p. 77): partly limestone and partly limestone-free siliceous stone. During the experiment it was placed in small cubic zinc boxes of 400 cm^3, with the bulb of the thermometer in the center. Four boxes with different humidity contents were used for each of the two kinds of gravel, but only 3 plots of each are given here.

The four pairs of plots (Diagrams 36, 37) are largely similar. In particular it is evident that siliceous stone, whether rock or gravel, is strongly warmed during full sunshine. The greatest difference with limestone in this respect lies in the gravel being *moderately moist*. This can perhaps be explained by a greater loss of heat due to stronger evaporation of water in the case of limestone, which is discussed below (p. 188).

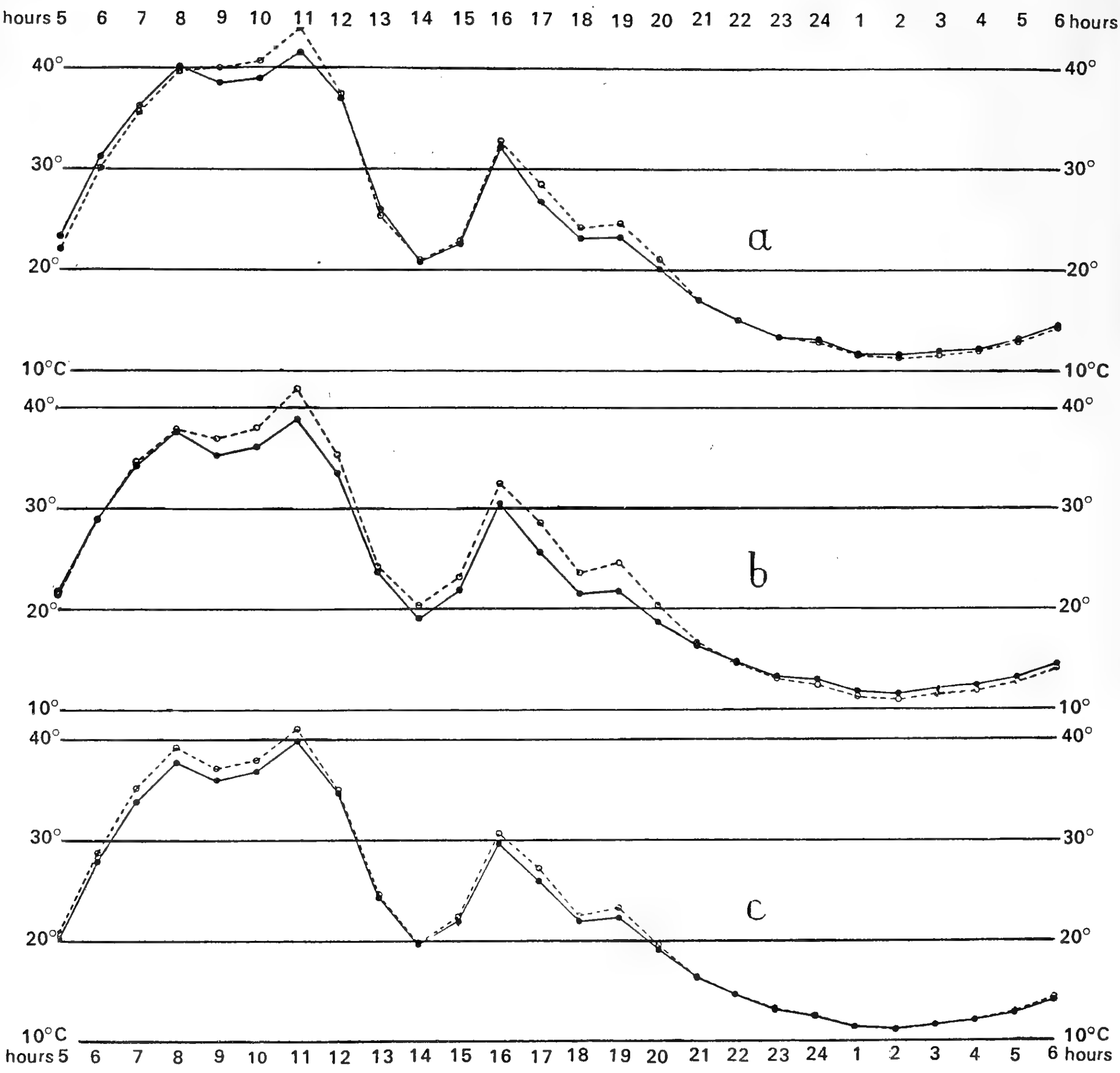
During the night the minima differ less. But it is obvious that those of limestone always lie a little higher (up to 0.6°C in moderately moist gravel). In the *gravel with the highest moisture content* the difference from siliceous stone is only 0.1°C.

It was evidently very important to test the general validity of the findings by further experiments, that is the higher temperature of the limestone by night, which, if borne out, would be of great biological significance. In the Fall (September 4 through October 29, 1945) the lowest night temperatures were measured with minimum thermometers in the same boxes placed in the
181 open with the gravel as dry as possible. Out of 54 readings higher values were shown by limestone in 31 cases, the values were identical in 20, and a difference of more than 0.1°C was recorded only in one case. The amounts of gravel used (400 cc) were very small.

I also wanted to study the temperatures of gravel under sudden heating or sudden cooling, and therefore recorded a series of readings at close intervals on a cold day after transferring the boxes of gravel, which had been outside for weeks, into the room. Later, the converse experiment was carried out (Experiments 156, 157). The temperature plots (Experiments 38, 39) show the same trend as in the 25-hour series (Diagram 37): With cooling, the temperature of siliceous stone always declines faster. With warming the same phenomenon was observed during the first half-hour (temperature rise of about 11°C); thereafter the temperature of the limestone always ran ahead (by up to 0.3°C). Identical temperatures were achieved after $3\frac{1}{2}$ hours only. Probably condensation heat was involved, which is more influential in the case of limestone due to the greater surface area (cf. evaporation plots, Diagram 41, p. 188). However, the precondition for this evidently was the complete drying of the limestone. For when the experiment was later repeated with the gravel cooled for only one day, both temperature plots showed exactly the reverse course to Experiment 157 (Diagram 39), i.e. the siliceous stone plot



179 Diagram 36. Twenty-five hour temperature plots underneath flat pieces of limestone and granite. Experiment 153, p. 110. Continuous line—Limestone; Broken line—Granite; Thin line—Temperature of air.



180 Diagram 37. Twenty-five-hour temperature plots in limestone gravel (continuous line) and siliceous gravel (broken line). Temperature of air and weather as in Diagram 36. a—Dry gravel; b—400 cm^3 gravel with 25 cm^3 water; c—With 100 cm^3 water. Experiment 154, p. 110.

constantly ran ahead.

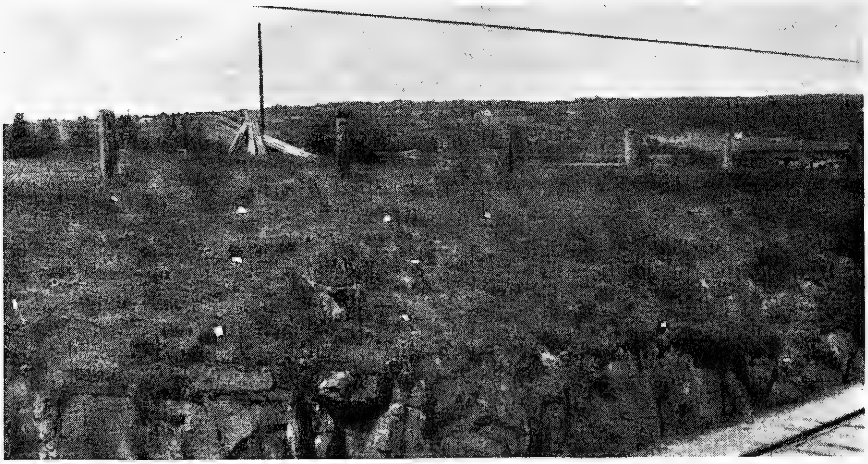
In all the temperature measurements here recorded for limestone and siliceous stone very small amounts were involved, moreover in unnatural locations. It was therefore deemed necessary to test the results in nature. Presupposition was that the temperature be measured simultaneously on limestone and siliceous stone *under as far as possible similar situations* (with respect to humidity, exposure to the sun and wind, etc.). Such requirements could be completely fulfilled only at a point where limestone and siliceous stone met edge to edge. Since such a situation hardly occurs in the case of loose deposits (moraine, fluvial rubble, etc.), it was necessary to find a suitable *fault fissure*. After consultations with several geologists Dr. P. Thorslund suggested a suitable area which he had studied some years before (Thorslund, 1936), namely, the railroad section near Sjurberg, north Rättvik in Dlr.

The location was visited on June 4–5, 1946 and measurements were taken.
184 All expectations were confirmed: The fault line is very sharp. The orthoceratite limestone and granite are not separated by any loose deposits, only the rock is brecciated in the immediate vicinity of the fault and is traversed by cracks (Fig. 16). The exposure on the two sides is exactly the same. The horizontal rock is overlain by a sandy limestone-containing moraine, which rises steeply from < 1 cm (at the edge of the profile) to a height of about 2 m. The slope is toward the east (12°N), thus receives the sun for almost the whole forenoon which is not impeded by any trees or bushes (Fig. 14).

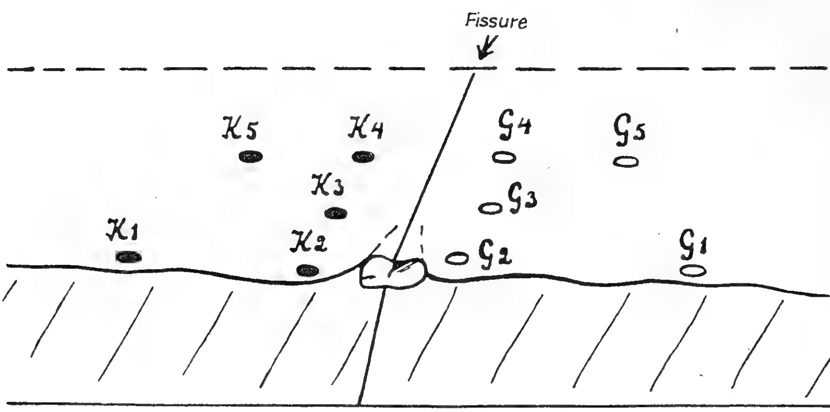
Here (Experiment 159) 5 thermometers were stuck (Fig. 15) in the ground (5–6 cm deep) in pairs on each side of and equidistant from the fissure, and the temperature was measured every hour from June 4, 5 p.m. through June 5, 7 p.m. The 4 thermometers along the edge (K_1, K_2, G_1, G_2) touched solid rock, the thermometers K_3 and G_3 were positioned over about 3 dm thick moraine and the 4 uppermost (K_4, K_5, G_4, G_5) over about 1 m thick moraine. There were no perceptible differences in the moisture content of the ground and vegetation.

The data obtained revealed striking differences. Those obtained with the thermometers K_2 and G_2 lying at the bottom of the fissure had to be omitted. Especially the plot of G_2, which was based on the strongly fissured and brecciated granite (see photo, Fig. 14), was greatly irregular. The 6 thermometers (K_{3-5}, G_{3-5}) sticking into thick moraine showed very small differences:

	K_3	G_3	$K_4 + K_5$	$G_4 + G_5$
Maxima	18.75	18.6	18.2	17.85
Minima	10.4	10.3	10.45	10.35



183 Fig. 14. Dlr Rättvik, Sjurberg. Place where temperature was measured on either side of the fault fissure. Ten thermometers are indicated by small pieces of paper. Experiment 159.



183 Fig. 15. Sketch showing the arrangement of thermometers in Fig. 14. K_1 to K_5 on limestone, G_1 to G_5 on granite. A granite block is seen at the mouth of the fissure.

It is evident that the identical moraine on both sides of the fissure has neutralized any probably existing thermal differences between limestone rock and granite rock.

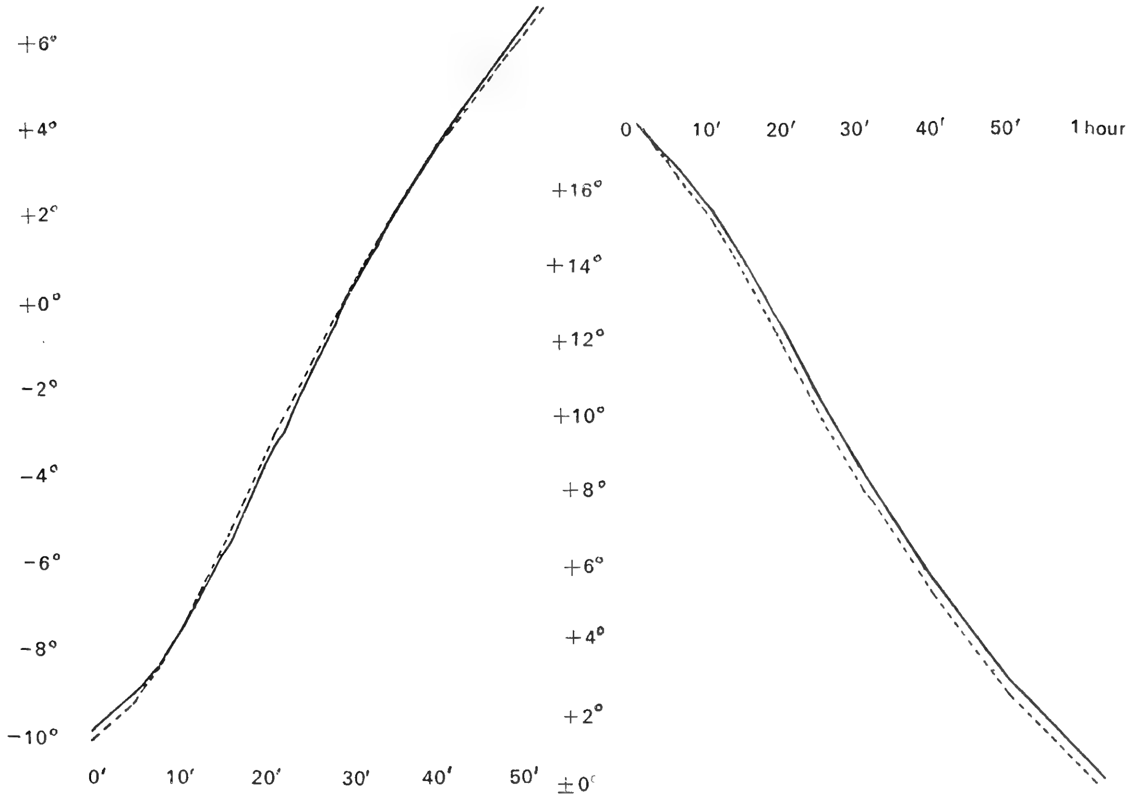
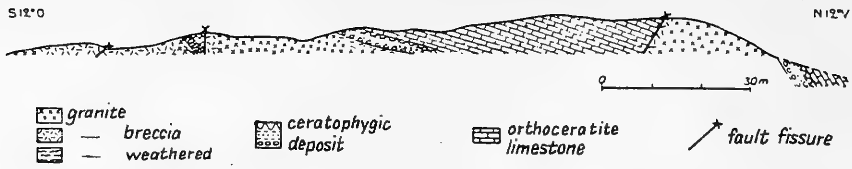


Diagram 38 (on the left). Course of temperature rise in limestone gravel (continuous line) and siliceous gravel (broken line) from –10.7° to +17.6°C after sudden transfer. Experiment 156, p. 111. Curves met only after 7 hours (at +16°C).

Diagram 39 (on the right). Course of temperature fall in limestone gravel (continuous line) and siliceous gravel (broken line) from +18.1° to – 6.1°C (gradually, down to –16.1°C) after sudden transfer. Experiment 157, p. 111. Because of the continuously falling in external temperature, curves never met during the period of observation (9 hours).

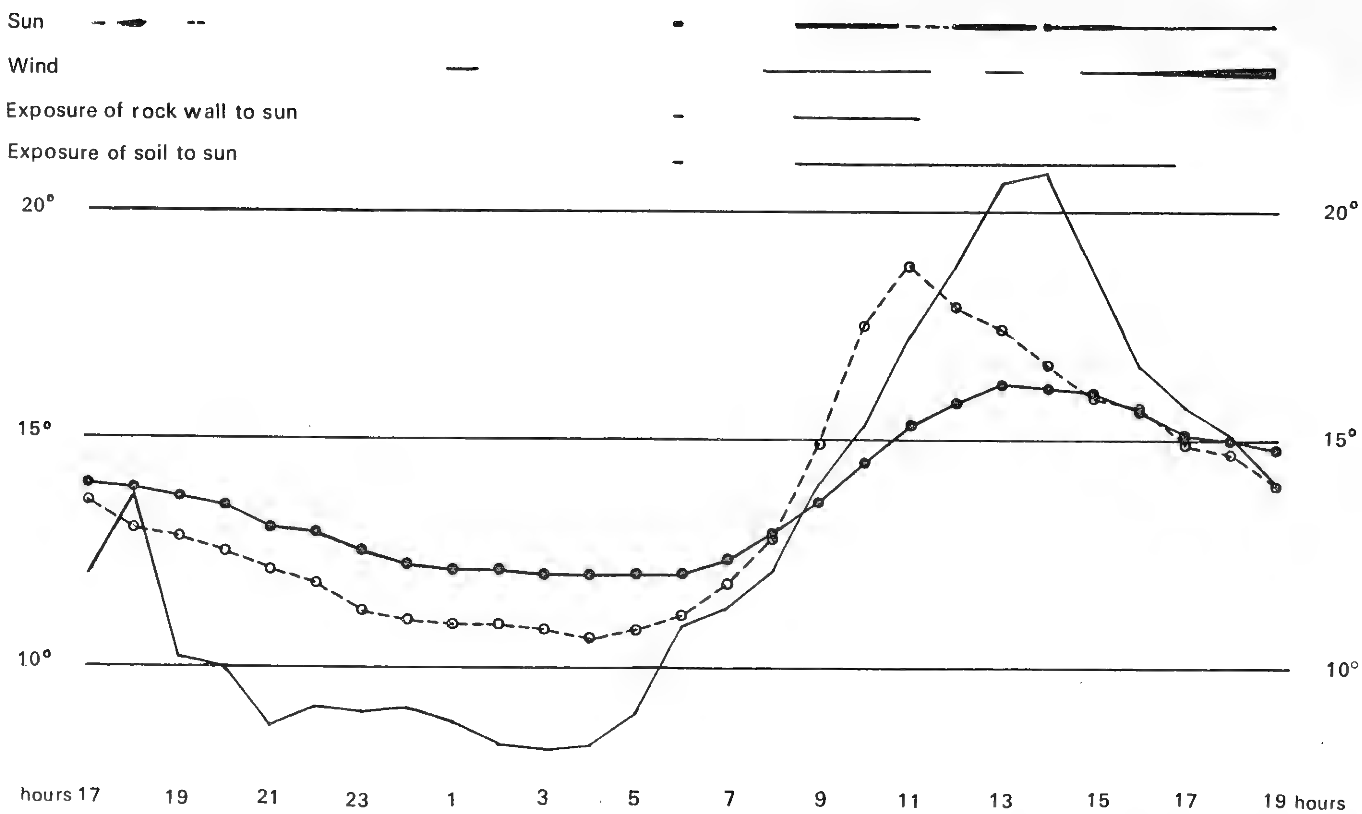


183 Fig. 16. Railroad section at Rättvik, Sjurberg. After Thorslund (1936, p. 7). Fault fissure ("förkastning") indicated in Figs. 14 and 15 to the right.

On the other hand the plots of the two thermometers K_1 and G_1 (Diagram 40) which touched the bedrock and were farthest from the fissure, consistently showed large differences. The maximum of the granite thermometer (18.8°C), reached 2 hours earlier, was 2.6°C above that of the limestone thermometer (16.2°C). But during the night, the *minimum temperature* of the latter was 1.4°C higher (10.6° as against 12.0°C). We thus have, on a larger scale, confirmation of the earlier conclusion obtained experimentally with small quantities of rock and gravel: *limestone shows lower maxima and higher minima, it provides an oceanic microclimate with regard to temperature* (!).

186 There is evidently a distinct thermal difference between the limestone (at any rate of Cambro-Silurian origin) and the basement complex (at any rate granite). Constants with respect to this are particularly found in the technical literature. The figures for specific heat are little different; in the case of granite and gneiss 0.20, in the case of limestone rock and marble 0.21 ("Hütte," 1931, p. 488; Suenson, 1942, p. 34). The thermal conductivity is different: In the case of granite and gneiss it is 2.7–3.5 kcal/degree m hr. ("Hütte," 1931, p. 494; Suenson, 1942, p. 35, gives 1.8 as the lower limit); in Sweden 3.0 is given as the mean value ("Anvisn. till byggnadsstadgan", 1946, p. 32); in the case of limestone rock, 0.6–0.8 according to "Hütte," 0.5–2.2 according to Suenson. *The limestone* (at any rate of Cambro-Silurian origin) *is a much poorer heat conductor than the basement complex.* We are also interested in the fact that marble is very close to the basement complex, since its thermal conductivity is given as 1.7–3.0 ("Hütte," l.c., Suenson, l.c.).

The different day plots of temperature on outcrop granite and limestone are thus undoubtedly due to the different thermal conductivity of the two kinds of rock. In the laboratory experiments with small quantities of material (Experiment 154; p. 178 above), dry and moderately moist gravel of siliceous stone and of limestone showed still greater thermal differences with regard to the daily maxima and minima. The pronounced differences in the thermal conductivity of *loose deposits,* which must also be present in nature, are undoubtedly due to the greater porosity and consequently the greater air content of the limestone gravel. Nevertheless, in nature this relationship can perhaps



185 Diagram 40. Dlr Rättvik, Sjurberg. 26-hour temperature plot, June 4–5, on both sides of fault fissure (cf. Figs. 14–16). Continuous line—On orthoceratite limestone (5–6 cm deep); Broken line—On granite; Thin line—Temperature of air.

never be verified as clearly as by the Rättvik plots on solid rock, since loose deposits (such as moraine) of *pure* limestone and *pure* siliceous stone hardly border on one another. However, it is justified to conclude *that the greatest thermal differences between limestone and the basement complex occur where on one side thin, loose limestone deposits* (especially purely residual soil) *rest on limestone rock, and on the other side where siliceous stone deposits rest on the basement complex.*

The data obtained near Rättvik, where the higher minimum temperature of 1.4°C on limestone has the main role biologically, must be considered as *minimal differences* for the following three reasons:

1. The adjoining solid volumes of limestone and granite are small (see profile by Thorslund, Fig. 16).

187 2. The loose deposits on both sides of the fissure are completely identical (limestone-containing moraine).

3. The weather before the readings were taken was very rainy all day. The ground was abnormally moist and as a result, extreme temperatures undoubtedly were more uniform (cf. the curves obtained in the laboratory experiments above, Fig. 37).

How little these things have been noticed until now is clear from the latest summary in the field of microclimatology, the work of Geiger, 1942. On p. 30 of this work the thermal conductivity of "cliff rock" is given as 0.011 cal/degree cm sec. without giving any amplitude! The literature, however, is full of different figures for the heat conductivity of various kinds of rock (cf. Stiny, 1929, pp. 436–437). The numerous readings of ground temperature by Kraus (1911) already show that the limestone content of loose deposits exercises a favorable thermal effect. But it may be added that Kraus strangely draws no general conclusions out of it. Otherwise literature frequently contains the statement that limestone is "warmer" (for instance, Thurmann, 1849, pp. 108–109; Warming-Graebner, 1918, p. 123; Hesse, 1924, p. 427; Brenner, 1930, p. 85), without substantiating the idea with data.

The above expositions are based on differences between limestone and siliceous stone with *identical humidity*. However, the natural conditions show, as has often been noticed by field botanists, that loose deposits of limestone or deposits with a big admixture thereof are *drier* than siliceous soil in the same situation. "Limestone plants" are therefore mostly evident as more or less markedly "xerophilous" (Thurmann, 1849, p. 268).

In order to test this difference more precisely, I performed a simple experiment (Experiment 158, p. 111; Diagram 41). Equal quantities (400 cm^3) of air-dried limestone gravel and siliceous gravel of the same particle size (types and quantities of gravel in boxes as in Experiment 154, p. 110) were mixed with 100 cm^3 water and kept in the room. Evaporation of the water, which was determined by recording the weight daily, was much faster in the case of limestone: 74.5% after 10 days. Within the same period only 50.5% water

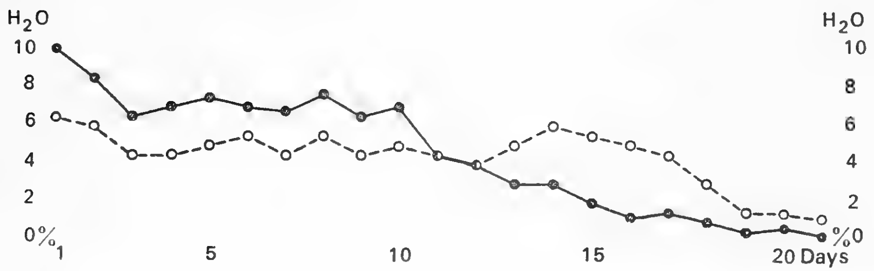
188 was lost by the siliceous stone. The reason is undoubtedly the flatter shape of the limestone particles (larger surface!) and the herewith connected greater porosity and aeration of the gravel mass.

Humidity then is of essential importance for the thermal conductivity of rock. Suenson (1942, p. 35) states: "In water-saturated condition granite, gneiss, marble, and limestone have approximately the same conductivity" (translated from the Danish). The faster evaporation and moreover the greater subterranean drainage in limestone, both reduce the thermal conductivity and by this increase the thermal difference when compared with silicates. Corresponding with this, the temperature plots in Experiment 154 (Diagram 37) with *wet* gravel were the least pronounced. *Hygrophilous animals are not favored on limestone.* Among such species only *Agonum krynicki, Bembidion clarki* and *B. lunulatum* have their northern Fennoscandian limits in areas with Cambro-Silurian limestone.

Effect of Limestone on Beetles

The experiments described and evaluated in the two preceding sections have shown that the "limestone species" are markedly xerophilous or (and) thermophilous animals and that limestone rock and loose deposits thereof in nature are comparatively dry, and particularly that they are thermally characterized by high minima of the ground temperature.

189 This latter characteristic is particularly significant for heat-requiring soil animals. It is for instance clear that all the species assumed here to be influenced by limestone live in Fennoscandia at the extreme northern boundary of their total area. Then it would not be too audacious to say that for them there is a definite problem of survival: how to attain a suitable hibernating



188 Diagram 41. Evaporation of water from equal quantities of limestone gravel (continuous line) and siliceous gravel (broken line) during 3 weeks. Experiment 158, p. 111. Each sample (400 cm^3) received 100 cm^3 water and was kept indoors.

stage during the short summer deficient in heat. In other words, the *length of the continuous period of life for these species may be especially decisive.*

We can now estimate the *length* of these periods (in days or weeks), thanks to the experiments on cold resistance (Experiments 125 ff., Diagram 20). But how this period is *utilized* in relation to the speed of development of the species in question can be revealed only by comparative breeding experiments. These are so far lacking. I must therefore content myself with an exposition of the first of these two aspects, by way of an example.

The meteorological measurements at the Visby station in Gotland, recorded over many years, make a suitable starting point. The thermometer for measuring the temperature of the air during this period (it was transferred to the harbor in 1937) was hung in a box 7.1 m above the ground on the wall of the posting house at "Donnersplan" close to the harbor. This house is situated on loose deposits below the steep limestone slope and is only a few meters above sea level. *The effect of the firm limestone rock and of the soil on the temperature was therefore very low*, and at any rate not of a "microclimatic" character.

The mean of the daily minimum temperature from April 10 through December 1 was calculated for the 20-year period (1917–1936) (Diagram 42). On the basis of this plot, the average continuous annual period of activity of each of the 16 tested species of *Harpalus* (of which only *neglectus, puncticeps,* and *rufitarsis* are missing in Gtl) was roughly calculated. The lower temperature limit of activity (Diagram 20, p. 130, "point b") determined by the cold resistance experiments (*aeneus* 5.2°C, *anxius* 3.4°C, etc.) was taken as the starting point.

The daily minima of the ground temperature (at a depth of about 5 cm) were calculated (at least for limestone the values are not too *favorable*!) according to the Rättvik plots (Diagram 40), both on limestone and on granite. One may now undertake a hypothetical analysis of the situation: *If*
191 *Gotland were made of granite instead of limestone*, how much lower would the minima of the ground temperature be? Or, more correctly, *how much shorter would the annual period of activity on granite be?*

Following the Rättvik plot we proceed from the hypothetical prerequisite that the minimum ground temperature (about 5 cm deep) on granite is 2.4°C and on limestone 3.8°C higher than the minimum temperature of the air. This gives us the above estimates (Table 8).

The average increase in the period of activity of all 16 species on limestone is 23.4 days. These values suggest *that an average increase in the minimum*
192 *ground temperature by only 1.4°C has great biological significance.*

I have also tried to depict cartographically (Fig. 17) the favorable effect of limestone ground on the basis of the Rättvik plots, an attempt of a purely hypothetical character. I used the map of the air temperature showing the mean
193 of the minimum temperature for May + September (Fig. 69, p. 471), adding 3.8° in the case of areas with Cambro-Silurian limestone, or 2.4°C in other

cases. These temperatures therefore hold good only for thin soil (5–6 cm) on bedrock*. Primitive limestone might well be equated with the basement complex, since the thermal conductivity of the two is almost the same (p. 186); the Mesozoic mountain materials (especially chalk) in southernmost Sweden, particularly in Skåne, are never exposed to the same extent.

The map shows the strikingly favorable temperature of the soil in Öland and Gotland, which is at best also attained in Skåne, and furthermore in the isolated Cambro-Silurian areas of Central Sweden, areas where *Harpalus ru-*

191 **Table 8. *Harpalus.* Average yearly periods of continuous activity on granite and limestone respectively, in a macroclimate of the Visby type. According to data in Diagram 20 ("point b") and diagram 40**

	On granite		On limestone		Increased duration on limestone
	Period	Number of days	Period	Number of days	
aeneus	1/5 — 8/11	192	20/4 — 22/11	217	25 days
anxius K	16/4 — 30/11	225	2/4 — 12/12	253	28 »
azureus K[1]	20/5 — 13/10	146	11/5 — 23/10	165	19 »
hirtipes K	11/5 — 24/10	166	1/5 — 7/11	190	24 »
melleti K	16/5 — 17/10	154	8/5 — 29/10	174	20 »
neglectus K	27/4 — 13/11	200	16/4 — 28/11	226	26 »
punctatulus K	17/5 — 16/10	152	8/5 — 27/10	172	20 »
puncticeps K	18/5 — 14/10	149	9/5 — 27/10	171	22 »
rubripes	10/5 — 26/10	169	30/4 — 9/11	193	24 »
rufitarsis K	14/5 — 20/10	159	5/5 — 2/11	181	22 »
rupicola K	19/5 — 14/10	148	10/5 — 25/10	168	20 »
seladon	10/5 — 25/10	168	1/5 — 8/11	192	24 »
serripes K	5/5 — 2/11	181	25/4 — 17/11	206	25 »
smaragdinus	23/4 — 19/11	210	11/4 — 4/12	237	27 »
tardus	11/5 — 24/10	166	1/5 — 7/11	190	24 »
vernalis K	13/5 — 21/10	161	4/5 — 4/11	184	25 »

[1]"Point b" of *azureus* (8.2°, Diagram 20) may actually lie still higher. In experiments with more material (20 specimens, Experiments 128, 129) the mean value of 10.8° was obtained. However, the difference on limestone and on granite here again would be 19 days (128 as against 109 days).

*The measurements recorded near Rättvik (see p. 181) indicate that the temperature in deeper loose deposits, even when composed chiefly of limestone, is more unfavorable than in thin soil resting on limestone rock, especially at night.

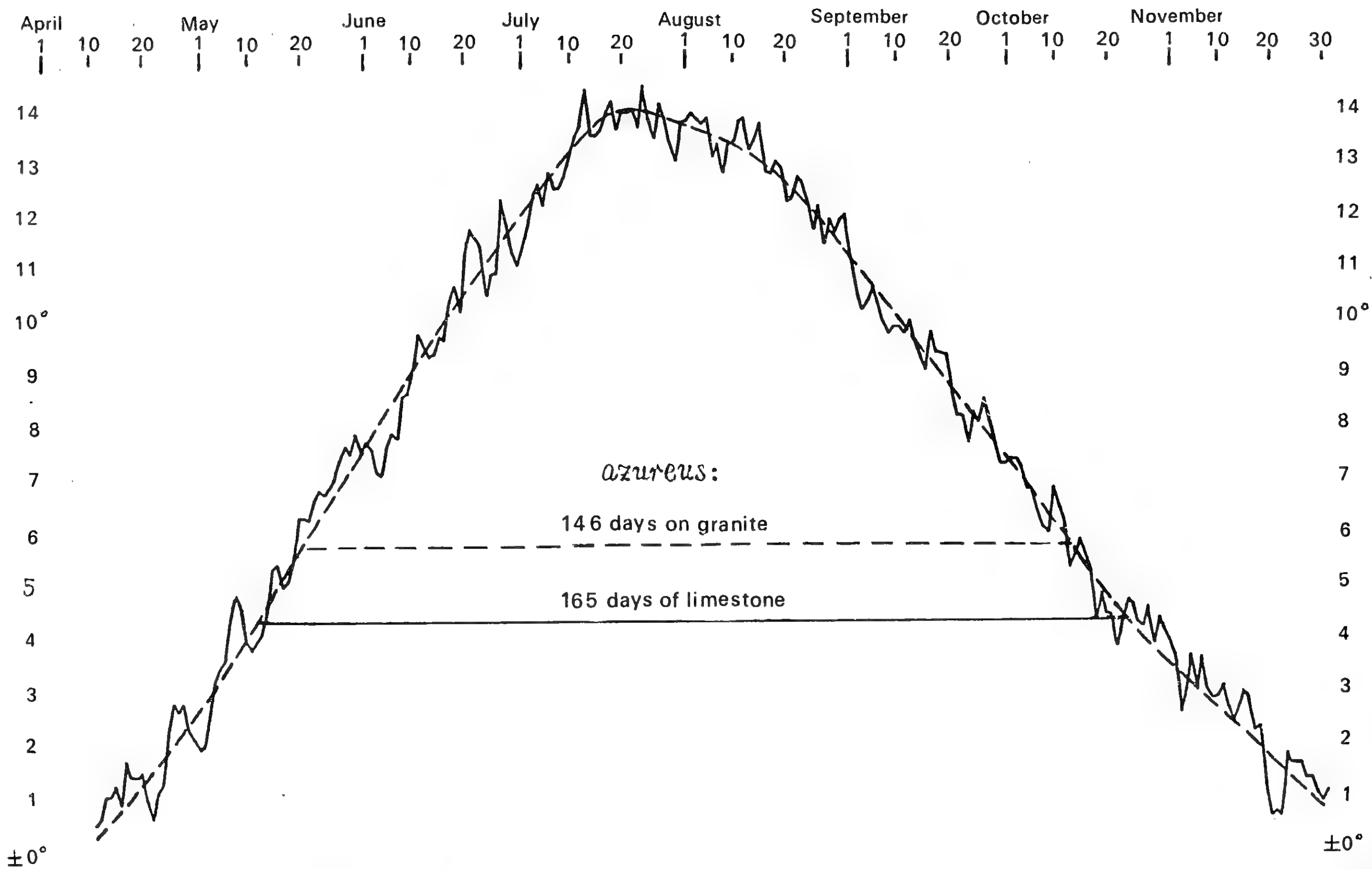
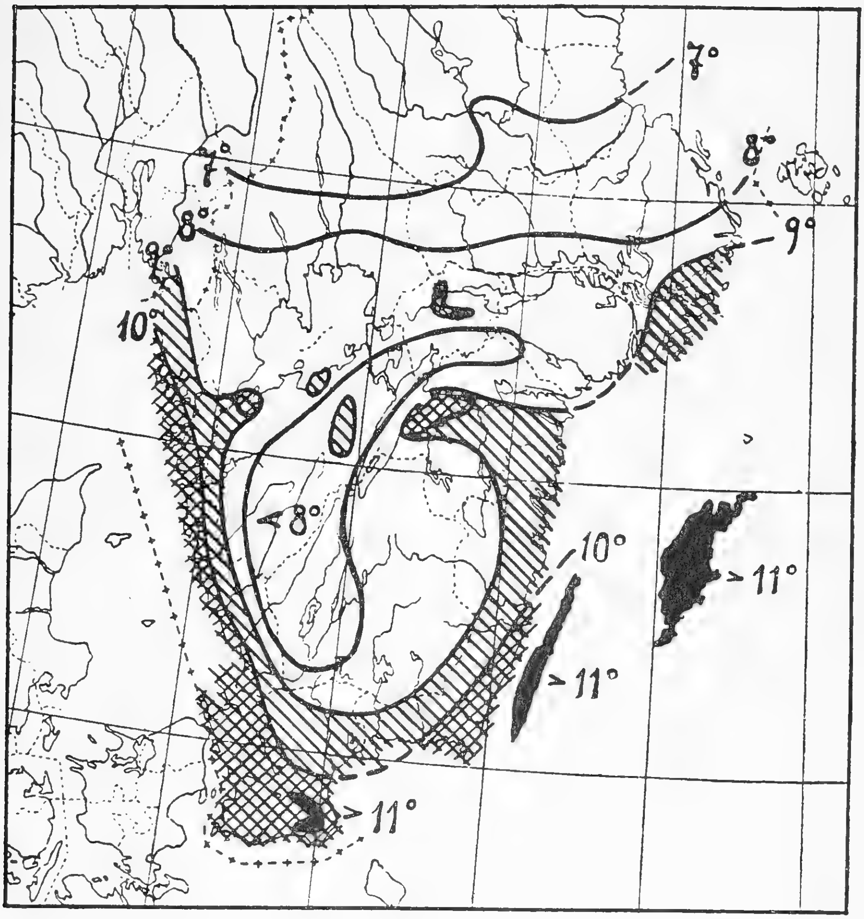


Diagram 42. Gtl Visby. Daily minimum temperature, mean of period 1917–1936. Empirical and balanced plot. Hypothetical annual periods during which *Harpalus azureus* would show full activity in the microclimate are marked with horizontal lines, on granite (broken line) and on limestone (continuous line). Calculations were made according to "point b" (Diagram 20, p. 130) and Rättvik plots (Diagram 40).

fitarsis, H. anxius, Panagaeus bipustulatus, Leistus rufomarginatus, Microlestes maurus, and *M. minutulus* have their relict-like northernmost occurrence.

It must seem daring (too daring?) to publish these two structures, the one in Diagram 42 and Table 8 and the other in the map just considered, on the basis of the Rättvik plots alone. However, I should emphasize again (cf. p. 186) that the temperature differences found near Rättvik must be considered as abnormally small. Besides, it is not known where in Sweden (but perhaps in southeastern Norway?) a location may be found that has a similarly favorable rock condition and could serve as an object of study. The geologists



192 Fig. 17. May + September. Hypothetical mean of the minimum temperature of the soil at a depth of 5–6 cm with bedrock immediately below. Cf. map, Fig. 69 (p. 471).

are not aware of any cases that can be compared with the Sjurberg fissure*. If generalization may be made, for which the biologist feels a strong urge, they must be based on very limited material and consequently be purely hypothetical. The intention was only to show that the thermal characteristics of the southern Swedish Cambro-Silurian limestone actually have an important biological role. The conclusion seems to be justified that these factors are decisive, especially at the periphery of the area of a soil-bound species, i.e. they may determine the northern limit in Fennoscandia.

It is noteworthy that the fairly rich occurrence of primitive limestone,
194 especially in central Sweden (Sdm, Upl, Vst, Dlr, etc.), for instance of *marble*, has no apparent influence on the soil fauna (however, it has on the flora). The south-facing slopes of the Kolmården mountains at the boundary between Sdm and Ögl, where marble occurs, show a strikingly poor fauna. The widely distributed but dispersed occurrence of limestone in Finland seems to exercise just as little direct influence on the insect fauna. This seems to be related to the fact that the occurrence of Cambro-Silurian deposits near Åland is only submarine (Metzger, 1927), whereas on the Finnish mainland only primitive limestone rock is found (Eskola, Hackman, etc., 1929).

Even areas that are characterized (Fig. 10, p. 115) by a striking admixture of *limestone in loose deposits* (moraine, diluvial gravel, etc.), but lack Cambro-Silurian outcroppings, for instance, in northern and western Upland (cf. map, Fig. 13, p. 123), are not characterized by any "limestone species" or "heat-requiring species" of the soil fauna.

Both these facts provide further weighty evidence against the assumption of a *chemical* effect of limestone on the beetles studied here.

Strangely, Holdhaus (1911a, pp. 742–743; 1911b, p. 342), in his study on the effect of rocks on the fauna of the Central and South European mountains, concludes that in the case of rock-bound (petrophilous) species "the chemical factors ... are more important [than the physical factors]," in spite of the fact that, with the exception of terrestrial snails, he could find no species of animals associated with a particular type of rock (1911a, p. 732). He of course implies a very indirect dependence (especially in the case of predators): "carnivorous animal—phytophagous animal—plant—soil (water)—rock" (p. 743), although he believes that the specific nutrient requirements of the animal is decisive. I cannot agree with him in this regard. Moreover, I am convinced that if his concept were correct, the distribution of animals on chemically different kinds of rock and soil would be far more defined and consistent. And, the carabids would not have turned out to be such distinctly polyphagous animals (see also p. 531).

The concept developed here, that limestone has no role as a chemical

*The Cambro-Silurian of the fjeld areas is markedly transformed, and even the limestone there is physically very different from that of southern Sweden.

factor for terrestrial insects—or only a subordinate role—would have received
195 substantial support from breeding experiments, by rearing the carabids and other "limestone species" from the egg, on a completely limestone-free substratum. I have repeatedly carried out such experiments, particularly with species of *Ophonus* (*azureus, melleti, punctatulus, rupicola*), but so far I have not managed to make these species oviposit, either on limestone-free or on chalky substratum. I hope the efforts of some more patient researchers will be rewarded with success.

Conclusions

The observations in nature and the experiments carried out on the effect of limestone ($CaCO_3$), at any rate on the carabids studied, justify the following conclusions:

1. The *chemical* characteristics of limestone are of no perceptible direct or indirect (e.g. through pH) importance.

2. The *physical* characteristics of Cambro-Silurian limestone are decisive. Among these, the effect of three groups of factors is noticeable:

a. *Thermally*, limestone is primarily characterized by *high minima of temperature*. For the animals investigated, *this is the most important characteristic of limestone*. Especially in Öland and Gotland, these and other thermal factors are intensified by the extensive horizontal surface of the limestone tableland, which is largely exposed to the sun, and by the small thickness of the overlying layer of weathered material. Furthermore, it must not be forgotten that flat limestone rocks are rapidly warmed through by the sun. Particularly in spring, this can be an important factor for insects buried underneath. Thus limestone favors *thermophilous* insects.

b. *Hygrically*, limestone is characterized by its *dryness*. This is the effect of several factors: Limestone rock has a tendency to form fissures and easily undergoes weathering, as a result of which downwards directed drainage is facilitated. Evaporation of water from the residual soil is rapid, since the particles are flat (with a large surface for evaporation) and irregular in shape, which results in high porosity with good aeration. —Thus *xerophilous* animals are favored on limestone.

c. *Mechanically*, low weight and flatness of the particles, as well as the
196 porosity of the soil arising from these two factors, are characteristic of limestone—thus burying animals (with a nocturnal mode of life) are favored.

This summary must lead to the conclusion that at least among the insects studied here (family Carabidae), none of the species can be called "*limestone-dependent*." In central Europe, there are certainly some other kinds of stratified rocks, which largely correspond with Cambro-Silurian limestone in their thermal, hygric, and mechanical characteristics. Holdhaus (1911a, p. 732), the only entomologist who seriously studied the dependence of animals on rock, also

claims that in the Alpine area, with the exception of the "calciphilous" terrestrial snails, there is no other species of animal occurring *only* on limestone. However, it is very probable that at the periphery of its area and also along its northern Fennoscandian limit, one or other species may live only on limestone for thermal reasons. According to our present knowledge, *absolute* dependence on limestone is found in insects only if a species is directly or indirectly dependent on a limestone-bound plant, which means secondary dependence.

Evidently we cannot apply our conclusions about insects to *autotrophic plants* without alterations. On the other hand there are certain responses common to all living organisms and not at least those against thermal factors. Hence it may not be presumptuous to ask the botanists too, especially the phytogeographers, to consider these entomological results. At present these researchers seem to consider the *chemical* effect of limestone as the main, if not the only, decisive area-limiting factor for so-called limestone plants.

In fact some botanists apparently regard the pH as the only decisive factor (Olsen, 1921, pp. 144, 145). It would be more prudent to regard it as an indicator (Lundegårdh, 1930, p. 350; Naumann, 1932, p. 10). Particularly in cases where a species of plant prefers soil with different pH-values in different parts of its area (for example, Pesola, 1928, pp. 208, 243), it would be interesting to find out whether *thermal* factors operate as well.

In this connection the well-known phenomenon might be recalled that certain species of plants are completely dependent on limestone only *at the*
197 *periphery* of their total area, chiefly along the northern limit* (Andersson and Birger, 1912, p. 44 ff.; Salisbury, 1920, p. 208) or at higher altitudes (Adamovic, 1909, p. 70). As true counterparts of our species of *Harpalus*, which require the most heat, we should not forget to investigate the "pure" species of plants occurring only in Öland and Gotland (enumerated on p. 298) with regard to their dependence on limestone and requirement of heat, particularly in the more southern areas. It would undoubtedly be productive if the phytogeographers made a new examination of Thurmann's old concept (1849) on the effect of the *physical* characteristics of soil on plants.

Study of these questions, however, demands the close cooperation of the field botanist and the laboratory botanist (preferably combined in one person). At present such a situation unfortunately does not exist within the domain of Swedish botany.

On the other hand the strong dependence of many plants on primitive limestone (for example, Eklund, 1931; cf. also Hope-Simson, 1938) also shows the undoubted effect of *chemical* factors, which, as far as is known, has no counterpart among insects.

*If a dependence on limestone along the *northern limit* can be explained by the higher night-time minima, it is conceivable that the lower day maxima of temperature on limestone (Diagrams 36, 37, 40) favor a *northern* species that is limestone-dependent only at its *southern limit.*

The Fauna of the Islands

An Example of the Significance of the Dynamic Properties of Animals

198 For the zoogeographer working on ecology there is hardly a more attractive task than to investigate the fauna of an island. The boundaries are drawn by nature and one need never doubt what should or should not be taken into consideration. The frequent pronounced poverty of fauna resulting from isolation and the limited number of biotopes permits the collection of sufficient material in a reasonable time. But the first question is: How did the animals get there?

We cannot apply the fundamental question of the origin of new species and what caused it in *our* islands. There is as little justification for classifying them as continental or oceanic. All of them lie on the continental shelf and even though a few, like Gotska Sandön, have as far as is known never been connected with the mainland, they basically do not differ, at least biologically, from the numerous islands in the Baltic Sea basin, which had such a connection only during the interglacial or preglacial periods.

On account of repeated Quaternary glaciations, biologically speaking, the Fennoscandian islands are very "young," for none of them completely escaped it. However, the paucity of very primitive ancient forms of animals on these islands has a certain advantage. We can estimate the maximum age of each member of our insular fauna without too many uncertainties; we can judge with fair certainty any changes in their area from the very beginning, possible land connections, climate, etc. In an area that underwent glaciation during the Quaternary period the islands show *the contemporary faunistic activity* almost as clearly as atolls emerging out of the sea. And thanks to the postglacial rising of the land, new islands are continually being formed even now.

199 The principal theme of this chapter is: *How does an island become populated?* And if it is possible to answer this question, at least for some cases or in a broad outline, then we will probably also be justified in trying to answer a general question: *How does a species of animal generally extend its area?*

The choice of islands whose carabid fauna is analyzed here in detail was on the one hand simple, on the other hand quite difficult. It was simple because

only islands whose fauna have been sufficiently explored could be considered and it was difficult because as many different types of island as possible had to be represented. In a few cases a compromise was unavoidable.

After some thought the following island regions were selected (see map in Fig. 18):

1. Hailuoto (Karlö) in Ob, in the northern part of the Gulf of Bothnia.
2. Åland (Al), main island.
3. The southwestern Finnish Skärgård between Åland and the Finnish mainland, eastward up to Ab Nagu.
4. Hogland (Ka) in the middle of the Gulf of Finland.
5. The remaining "outer islands" in the Gulf of Finland: Tytärsaari, Lavansaari, and Seiskari.
6. Valamo (Kl), in Ladoga.
7. Värmdö-Ingärö and Djurö (Upl), in the Skärgård of Stockholm.
8. Ösel and Dagö (situated outside the region).
9. Gotska Sandön, North of Gotland.
10. Fårön, immediately northeast of Gotland.
11. Gotland (excluding Karlsoarna).
12. Öland.
13. Bornholm (situated outside the region).
14. Ven (Skå), in Oresund.
15. Islands in the Skärgård of Göteborg (Vgl, Boh): Brännö, Styrsö, Donsö, Öckerö, and Hönö.
16. Orust, in the middle of the province of Bohuslän (Boh).
17. Hvaler (1), on the Swedish border.
18. Hitra and adjoining islands (9, 26), west of Trondheim.
19. Dönna, Alstenöy, Heröy, and Lökta (31).
20. Lofoten and Vesterålen (the whole of Province 34) in northwestern Norway.

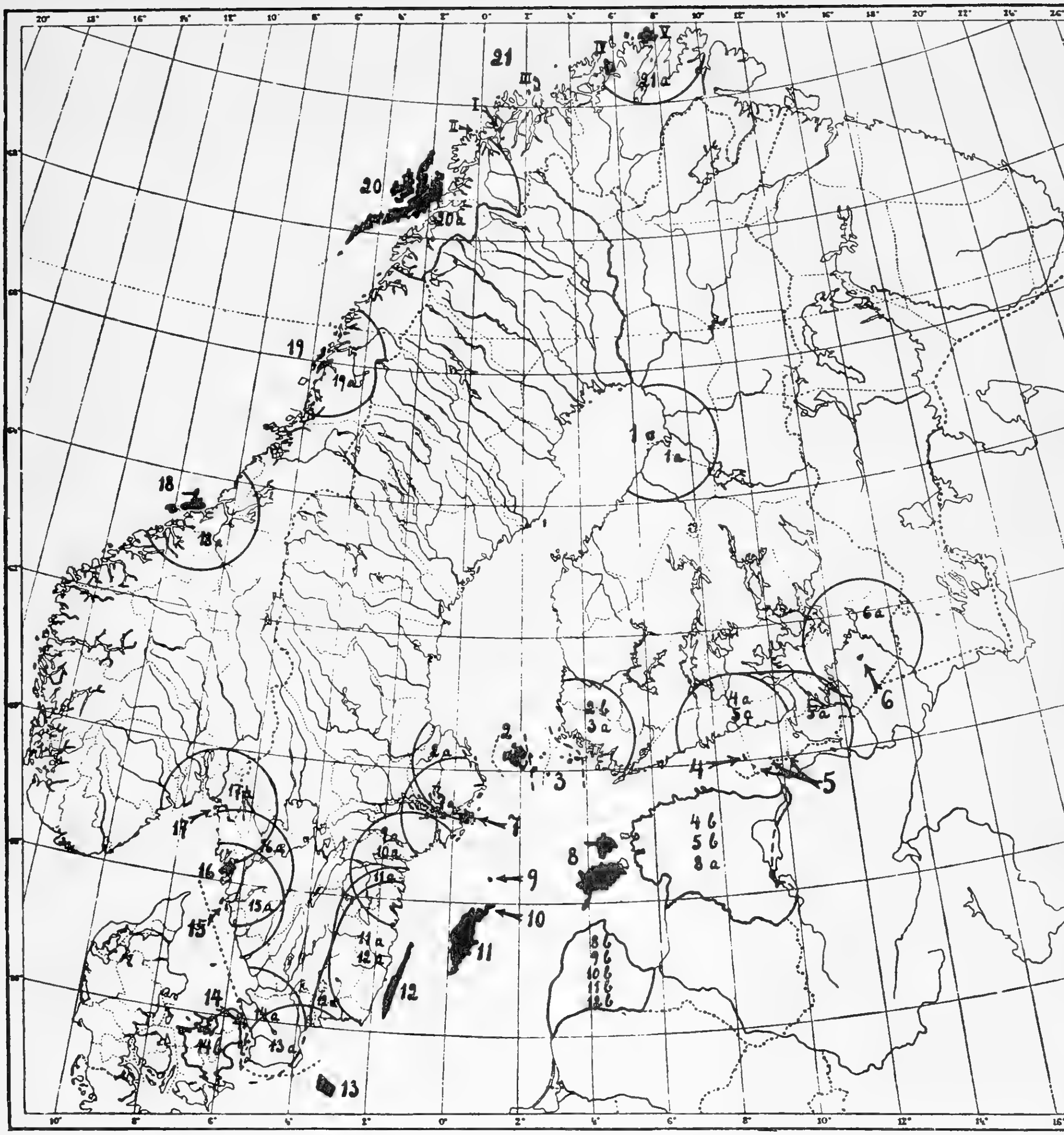
201 21. Five islands in Troms and Finnmark. These are not considered in the following tables because their inclusion would be unnatural.

It was unfortunate that the Solovetsk islands in the White Sea have been studied too little to be considered. But fortunately the islands selected form a diverse collection. The following are the most important variations:

a. *Size*. The largest island, Gotland, is 2960 km^2, and the smallest, Ven, is 7.5 km^2 (some islands in the groups of islands considered are even smaller).

b. *Isolation*. Fårön is farthest from the mainland (125 km) but it is only 0.5 km from Gotland. The greatest *absolute* isolation is that of Gotska Sandön, with 38 km of distance from any other land. The outer Finnish islands and Bornholm are also quite isolated.

c. *Variety of biotopes*. The greatest uniformity is shown by the outer islands in the Gulf of Finland, which are made of moraine or quicksand, and by Gotska Sandön. They almost totally lack fresh water and are therefore uninhabitable



200 Fig. 18. Islands studied and regions on mainland compared with them (a, b).

1—Hailuoto; 2—Åland; 3—Skärgård east of Åland; 4—Hogland; 5—Remaining "outer islands" in the Gulf of Finland; 6—Valamo (in Ladoga); 7—Värmdö-Ingarö and Djurö; 8—Ösel and Dagö; 9—Gotska Sandön; 10—Fårön; 11— Gotland; 12—Öland; 13—Bornholm; 14—Ven (in Öresund); 15—Skärgård of Göteborg; 16—Orust; 17—Hvaler; 18—Hitra, Smöla, Dolmöy and Fröya; 19—Dönna, Alstenöy, Heröy, and Lökta; 20—Lofoten and Vesterålen.

I–V—5 islands of Northern Norway: I—Tromsö; II—Hillesöy; III—Nordfu,-löy; IV—Kvalöy; V—Mageröy.

for many hygrophilous species. Moreover Ven, the islands in the Skärgård of Göteborg and those in northernmost Norway are markedly uniform. The most vivid variety of biotopes is shown by the biggest islands, especially Åland and Gotland.

d. *Age*, not geological but *biological*. In this sense some of the West Norwegian islands are the oldest: probably they were partly outside the ice cover during the last glaciation, and were never flooded during the postglacial period. In the Baltic Sea area only Hogland and Bornholm appeared as islands immediately after the ice melted. The youngest, also geologically speaking, are Hailuoto and two of the Finnish outer islands.

e. *Postglacial land connection*. Such a land connection did *not* exist for any Baltic Sea island north of about 59° N latitude. This assumption is much disputed for the islands lying south of this. Such a land connection has been generally assumed only for Bornholm and Ven. —The fauna of the West Norwegian islands may have partially survived *in situ* during the entire period after an inter-glacial land connection.

f. *Ice corridor during winter*. Biologically speaking such a connection can replace a land connection to a limited extent. In the Bothnian Sea such a firm land corridor is an annual phenomenon, but in the remaining Baltic Sea
202 region as well as on the Swedish west coast such a corridor is formed only in especially severe winters. It is never formed along the Norwegian Atlantic coast.

g. *Influence of man*. Unfortunately none of the islands considered is completely uninhabited. However the influence of human culture on the Finnish outer islands, on Gotska Sandön, and on some tiny islands in northernmost Norway is minimal.

The characteristics of each island or group of islands, in this and other respects, are described below along with an analysis of the fauna.

A comparison between two or more different insular faunas should not be undertaken just to determine the common and peculiar species (Table 9). A more rewarding insight into the faunal character of a region is obtained by dividing the species into different ecological, dynamic and other groups (Tables 10, 12–14). But even the results so obtained must be used with caution. For instance, it could easily be imagined that the absence or presence of a species (or an entire group of species) capable of flight depends on its ecology, and that this is a decisive factor, whereas the flight capacity is of minor importance. This is true to a certain extent. Hygrophilous species, particularly nearly all of the ripicolous fresh-water forms, have well-developed wings. So on an island, which lacks such bodies of water, a decrease in the percentage of species capable of flight could be expected. —The xerophilous component in the fauna decreases going north, the flightless species become more common toward the west, and the same is true of the species that hibernate as larvae. Hence a comparison of the dynamical, ecological and other groups from the

islands alone would be subject to too many sources of error.

For a more reliable criterion for deciding what is "normal" and what is peculiar in one or other insular fauna, *regions of comparison*, shown in the map (Fig. 18), were selected on the mainland. They were generally demarcated as circles with a radius of 100 km each, the center at the coastal point closest to the island. In the case of long island (Öland, Gotland) or widely separated islands (outer islands in the Gulf of Finland), the region of comparison was correspondingly increased in length. Irregularly formed regions of comparison are Estonia, Kurland, and Sjaelland, where the extact localities of some species were not known. For the same reason a desirable region of comparison could
203 not be found in North Germany for Bornholm. I did not let the regions 19a and 20a in northwestern Norway overlap the Swedish fjelds, since they are unsuitable for comparison, and for that reason (in 20a) the diameter of the regions was correspondingly increased. Most of the Baltic Sea islands, as well as Ven in Öresund, were assigned *two* regions each of comparison.

It is necessary to emphasize that the regions of comparison were not selected as the presumed areas of origin of the insular fauna concerned. They were intended only to show how the fauna has evolved under as similar conditions as possible but *with better possibilities of immigration*, and to serve as a standard against which the peculiar character of the insular fauna stands out more sharply.

Some islands situated far outside the region in the North Sea and in the northern Atlantic were also considered for the purpose of comparison (Table 25). They are discussed at the end of this section (pp. 325 ff.).

Before we pass on to a study of the individual insular regions it is advisable to give some more tabulated survey to facilitate comparison.

It is imperative to form a judgment on the *capability of dispersal*† (*the dynamics*) of the insular beetles. The easiest way to do this is to divide the species into "flight groups" (m, b, d, etc.) as in Table 10.

In contrast with the areas of comparison most of the islands are constantly deficient in macropterous species. This is surprising, since the numerous species appearing more or less accidentally on the islands mostly belong to this group. Only the outer islands in the Gulf of Finland and Gotska Sandön show a clear preponderance of such species. The brachypterous species constantly occur in about one-half the number of islands with plus or minus values. However, the most characteristic feature is *the large component of dimorphic species in the insular faunas*. Only Hailuoto Island shows slightly minus values. Nevertheless, in the case of this island, the region of comparison (1a) has the largest number of dimorphic species of all, resulting in that the number of the island itself is relatively but not absolutely low.

†(Contradictory to the ecological term "dispersion"; cf. p. 53; suppl. scient. edit.).

This large element of dimorphic species, which on different islands is between 15.6% (Gotska Sandön) and 26.4% (Orust), is functionally quite heterogeneous. Such a species may occur in one region exclusively in macropterous form, in another in brachypterous form, or it may even be dimorphic in the
204 region in question. So a reliable division of the insular carabids was not possible without a study of the representative material of the dimorphic forms from all the islands. Such material was not available from Ösel and Dagö, which had to be omitted in the following tables. An account of all the specimens of dimorphic insular carabids examined is given in Table 11.

We are now in a position to provide a reliab e tabulation (Table 12) of the dynamic groups of insular carabids. The regions of comparison are taken into consideration but it must be emphasized that the data on these are only estimates, since complete material from all the regions of comparison could not be studied. However, the resulting errors cannot be large, since both forms of a dimorphic species are distributed on the mainland far more regularly than on the islands.

The most important figures in Table 12 are the percent deviations from the regions of comparison especially the column "b + d," that is, the *sum of the species found to be brachypterous and dimorphic in the area concerned.* In the case of the latter the macropterous form is generally far more rare than the brachypterous form, and if the material studied is too small, often the former may not be proved at all. In this connection Bornholm offers a clear example. The number of species found there only in brachypterous form (column "b") is much larger than on Öland and Gotland, since insufficient material was available. On the other hand the sum of "b" and "d," which undoubtedly corresponds better with reality, is somewhat smaller on Bornholm.

The study of the dimorphic forms in the following section will show that the brachypterous form can immigrate through the macropterous form rarely if ever (either through a macropterous female that has already copulated with a brachypterous male, or by recurrent mutation). It is therefore valid to consider a dimorphic species that occurs in the region concerned exclusively or partly in brachypterous form as functionally belonging to the dynamic group of brachypterous species. This group shows the highest numbers (both absolute and relative) on the islands along the Norwegian west coast and the lowest on Gotska Sandön and the outer islands in the Gulf of Finland.

205 The brachypterous group (b + d) in Table 12 is of particular interest from the viewpoint of the history of immigration. They include species whose dispersal was especially difficult and for which air passage is virtually impossible (see also p. 590). Besides being passively dispersed by man or by animals they were able to colonize most of our islands by passive transport with water and ice, since, with few exceptions, there has been no land connection during the postglacial period.

Obviously such accidental transport can only lead to successful permanent

colonization of a particular island where possibilities exist for breeding. This is dependent not only on the presence of a suitable biotope but also on the essential prerequisite that either an impregnated female reaches the island, or two or more individuals arrive more or less simultaneously so that pairing can take place in the new region. The latter possibility might be applicable especially in the case of dimorphic species, when a brachypterous individual that has arrived by one or other method is able to pair with a wind-transported specimen of the macropterous form. The pronounced occurrence of dimorphic species in the insular faunas (Table 10) can perhaps be explained this way.

At any rate, transportation of imagines must be much more advantageous than that of larvae (or other immature stages). In view of their weak chitinization, the latter are more susceptible in every way, especially to changes in the humidity of the air and substratum. Compared with imagines their concealed mode of life seldom exposes them for passive dispersal.

The above considerations suggest that the colonization of an island by any species takes place mainly in the season when it is adult. In this respect our carabids in no way exhibit identical behavior. Most of them are indeed adult hibernators (with spring breeding), but a few are quite irregular and seem to be able to hibernate at almost every stage. Finally there is a fairly large group (increasing toward the west) of 72 species (20% of the Fennoscandian fauna) that hibernate only or normally as larvae (cf. p. 568).

It seems to be correct to take passive transport by water as the most important mode of colonization of islands by flightless species. To answer
234 the question whether this transportation occurs mostly in the winter half-year (with drifting ice), especially in early spring, or in summer, we need to know whether the brachypterous and truly dimorphic species of one or other island (and the "regions of comparison") are mainly adult or larval hibernators. If the latter, winter transport would seem to be of lesser importance.

Table 13 was prepared to provide a firmer basis for such considerations. It classifies the flightless and (in the region concerned) dimorphic species into more or less pronounced larval hibernators [O + L + (L), see Table 9] and exclusively or predominantly imago hibernators [I + (I)]. The relationship between the sum of both groups of species (fourth and eighth columns) is expressed as an index number (ninth column). More important is the deviation from the index number of the regions of comparison (tenth column).

Finally, it is naturally of special interest to undertake an *ecological* grouping of the insular carabids (Table 14). It is not only an expression of the biotope characteristics of the island itself, but may occasionally also provide a clue to the origin and the immigration route not of the entire fauna, but of one or other species. Keeping in view the frequent occurrence of accidental, wind-driven migrants on the islands, which do not belong to the native fauna of the island concerned (see f. ex. Gotska Sandön, p. 282), which on the other hand cannot consistently be omitted, it seemed to me best to consider in this

case only the brachypterous species and the "true" dimorphic species (b + d, Table 12). The reduced reliability of the data resulting from the smaller number of species is perhaps compensated by the elimination of all accidental migrants. The ecological groups and symbols (x, n, h, etc.) are those used in Table 9. In the last two columns, the percentage deviations from the regions of comparison have been especially noted in the case of xerophilous and forest species.

Details of the six tables given below are discussed more fully in the following separate treatment of each insular region.

206–221 **Table 9. List of carabids found on Fennoscandian islands studied**

Presence of species on an island (or island group) is indicated by + and absence by –. In the first 3 columns species are grouped as follows:

A. Dynamic groups

m—Constantly macropterous species; flight observed; (m)—Constantly macropterous species; flight not observed: b—Constantly brachypterous and flightless species; d—Dimorphic species; macropterous form observed in flight; (d)—Dimorphic species; flight not observed.

Dimorphic species found in Fennoscandia only in one form, macropterous or brachypterous, are listed with this group (=A.)

B. Hibernation groups

I—Constantly adult hibernator; (I)—Predominantly adult hibernator; I^2—Adult hibernator in the north, probably with 2-year development; L—Constantly larval hibernator; (L)—Predominantly larval hibernator; L^2—Larval hibernator in the north, probably with 2-year development; O—Species with irregular hibernation, i.e. both stages (larva and adult)

C. Ecological groups

x—Strongly xerophilous; (x)—Weakly xerophilous; n—Mesophilous (including ecologically ubiquitous species); (h)—Weakly hygrophilous; h—Strongly hygrophilous; a—Arboricolous; w—Pronounced forest species; (w)—Predominantly forest species; k—Exclusively synanthropous species

	Dynamic group	Hibernation group	Ecological group	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remaining outer islands	6 Valamo
Acupalpus consputus	m	I	h	—	—	—	—	—	—
A. dorsalis	m	I	h	—	+	+	+	+	—
A. exiguus	m	I	h	—	+	+	—	—	—
A. flavicollis	m	I	h	—	+	—	—	—	—
A. meridianus	m	I	n	—	—	—	—	—	—
Aëpus marinus	b	L?	h	—	—	—	—	—	—
Agonum assimile	m	I	(h) (w)	—	+	—	—	—	—
A. consimile	m	I	h	—	—	—	—	—	—
A. dolens	m	I	h	—	+	—	+	+	—

235 **1. Hailuoto (Karlö)**

This island, Finland's third-largest, now has a surface of about 170 km^2 (in 1933; Paasivirta, 1936, p. 72); however, because of the pronounced rising of the land (about 10.5 mm per year; Witting, 1943, p. 28) it is continuously increasing. As late as the beginning of the 19th century it comprised three (originally four) separate islets (Sandman, 1892, p. 190). The greatest height, in the north, is about 30 m above sea level. The greatest age of the island is estimated at about 2000 years (Rosberg, 1893, p. 3). The shortest distance from the mainland (of the Oulunsalo Peninsula) is 9 km; it is 10 km from the southern end of the island.

The variety of biotopes is striking (Sandman, l.c.). The main part (78.6% according to Paasivirta, 1936, p. 81) is occupied by forest. But its character is quite variable: the higher gravel ridges are occupied by pines, the lower parts by spruce and in the south there is also a rich covering of mixed forest. Meadows of leaves ("Laubwiesen") are also found here. In the interior there are numerous small lakes, some of which have been transformed into moors (including those with species of *Sphagnum*) or swamps. In the southern part some of the lakeshores are richly vegetated (*Phragmites*, *Scirpus lacustris*, etc.). There is no rocky ground. Some of the seashores are meadowlike, some more or less barren, stony or sandy. Especially in the west there are quicksand regions (Krogerus, 1932, p. 86 ff.).

The population (at least 2300 in 1933; Paasivirta, 1936, p. 80) is entirely concentrated in the southern and eastern parts. There is daily ship contact with Uleåborg. Earlier (before construction of the railroad to Uleåborg) the island was "an important trading center for freight vessels" (l.c., p. 94).

The *carabid fauna*, which has not been thoroughly explored, comprises

7 Värmdön etc.	8 Ösel and Dagö	9 Gotska Sandön	10 Fårön	11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.
–	–	+	+	+	+	+	–	–	–	–	–	–	–
–	+	+	+	+	+	+	+	+	–	+	–	–	–
–	–	–	+	+	+	+	–	–	–	–	–	–	–
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–	+	–	–	–	+	+	+	+	+	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	+
–	–	–	–	–	–	+	–	–	–	–	–	–	–

	Dynamic group	Hibernation group	Ecological group	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remaining outer islands	6 Valamo
Agonum dorsale	m	I	(x)	—	—	—	—	—	—
A. ericeti	b	I	h	—	—	—	—	—	—
A. fuliginosum	(d)	(I)	(h) (w)	—	+	+	+	+	+
A. gracile	m	I	h	+	+	+	+	+	+
A. gracilipes	m	I	(x)	—	—	+	—	—	—
A. krynicki	(m)	I	h w	—	—	—	—	—	—
A. livens	m	I	h (w)	—	+	—	+	+	—
A. lugens	m	(I)	h	—	+	+	—	—	—
A. mannerheimi	(m)	I	h w	—	—	—	—	+	—
A. marginatum	m	I	h	—	+	—	+	+	—
A. micans	m	I	h	—	—	—	—	—	—
A. moestum	d	I	h	—	—	+	—	—	—
A. mülleri	m	I	(h)	—	+	+	+	—	—
A. obscurum	(d)	O	h (w)	—	+	+	—	—	—
A. piceum	m	I	h	—	+	—	+	—	+
A. quadripunctatum	m	I	n (w)	—	+	+	+	—	+
A. ruficorne	(m)	I	h	—	—	—	—	—	—
A. sexpunctatum	(m)	I	(h)	+	+	+	+	+	+
A. thoreyi	m	(I)	h	—	+	+	+	—	+
A. versutum	m	I	h	—	+	—	—	—	—
A. viduum	m	I	h	+	+	+	+	+	+
Amara aenea	m	I	x	—	+	+	+	+	+
A. apricaria	m	(L)	n	+	+	+	—	+	+
A. aulica	m	L^2	n	—	+	+	+	—	+
A. bifrons	m	L	(x)	—	+	+	+	—	—
A. brunnea	(m)	(L)	n (w)	—	+	+	+	—	+
A. communis	m	(I)	n	+	+	+	—	—	—
A. consularis	m	L	(x)	—	+	+	—	—	—
A. convexiuscula	(m)	L	(h)	—	—	—	—	—	—
A. crenata	m	I	n?	—	—	+	—	—	—
A. cursitans	(m)	(L)	n	—	—	—	—	—	—
A. curta	(m)	I	(x)	—	+	+	+	—	+
A. equestris	(m)	L	(x)	—	+	+	—	+	—
A. erratica	(m)	I	n	—	—	—	—	—	—
A. eurynota	m	I	n	—	+	—	—	—	—
A. famelica	(m)	I	(h)	—	+	—	+	+	—
A. familiaris	m	I	n	+	+	+	+	+	—
A. fulva	m	L	(x)	+	+	+	+	+	—
A. fusca	(m)	L	(x)	—	—	—	—	—	—
A. infima	(d)	I	x	—	—	—	—	—	—
A. ingenua	m	I	n	—	+	—	—	+	—
A. interstitialis	m	I	n	—	—	—	—	—	—

7 Värmdön etc.	8 Ösel and Dagö	9 Gotska Sandön	10 Fårön	11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.
−	−	−	−	+	+	+	+	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	+	−	+	−	−
+	+	−	+	+	+	+	−	−	−	−	+	+	+
−	−	+	−	+	+	+	+	+	−	+	−	−	+
−	−	+	+	−	+	+	−	−	−	−	−	−	−
−	−	−	−	+	+	−	−	−	−	−	−	−	−
+	−	+	−	+	+	+	−	−	−	−	−	−	−
−	+	−	−	+	+	+	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	+	−	+	+	+	+	−	+	+	+	−	−	−
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−	−	−	+	+	+	+	−	−	+	+	−	−	−
+	+	−	+	+	+	+	+	+	+	+	−	−	−
+	+	−	+	+	+	+	+	−	+	+	−	−	−
−	−	+	+	+	+	+	+	+	−	+	−	−	−
−	−	+	+	+	−	+	−	+	−	−	−	−	−
+	−	−	+	+	+	+	+	+	−	−	−	−	−
+	+	+	+	+	+	+	−	+	+	+	−	−	−
+	+	+	−	+	+	+	+	−	−	+	−	−	−
−	+	−	−	+	+	+	−	−	−	+	−	−	−
+	−	−	−	+	+	+	−	+	+	+	−	−	−
+	+	+	+	+	+	+	+	+	+	+	−	−	−
+	+	+	+	+	+	+	+	+	+	−	+	+	+
+	+	+	+	+	+	+	−	+	+	−	+	+	+
+	+	+	+	+	+	+	−	+	+	+	+	+	+
+	−	+	+	+	+	+	−	−	−	+	−	−	+
+	+	−	−	+	+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	−	+	+	−	−	−	−
−	−	−	−	+	+	+	+	+	−	+	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	+	+	+	−	−	−	−	−	−	−
−	+	−	+	+	+	+	−	−	−	+	−	−	−
+	−	−	−	+	+	+	−	−	−	+	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+
−	+	−	−	+	+	−	−	−	+	+	+	−	−
+	−	−	−	+	+	−	+	−	−	−	−	−	−
+	+	+	+	+	+	+	+	+	+	+	+	−	+
+	+	+	+	+	+	+	−	+	−	+	−	−	−
−	−	−	−	−	−	+	+	−	−	−	−	−	−
−	+	−	−	−	+	+	−	−	−	−	−	−	−
+	−	+	+	+	+	−	−	+	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	+	+

	Dynamic group	Hibernation group	Ecological group	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remain-ing outer islands	6 Valamo
Amara littorea	(m)	I	n	—	—	—	—	—	—
A. lucida	(m)	(I)	(x)	—	—	—	—	—	—
A. lunicollis	m	I	n	—	+	+	+	—	+
A. majuscula	m	L	n	—	+	+	—	+	—
A. municipalis	m	(L)	n	—	+	—	—	—	—
A. nitida	(m)	(I)	(x)	—	+	—	—	—	+
A. ovata	m	I	n	—	+	+	+	—	—
A. plebeja	m	I	(h)	+	+	+	+	+	+
A. praetermissa	m	L[2]	(x)	—	+	+	—	—	—
A. quenseli	(m)	O	x	+	—	—	—	—	—
A. similata	m	I	n	—	+	+	+	—	+
A. spreta	m	I	(x)	—	—	—	—	—	—
A. tibialis	m	I	(x)	—	+	+	+	—	—
A. torrida	(m)	O?	n	—	—	—	—	—	—
Anisodactylus binotatus	m	I	(h)	—	+	+	+	—	—
Asaphidion flavipes	m	I	(h)	—	—	—	—	—	—
A. pallipes	m	L	(h)	—	—	—	—	+	—
Badister bipustulatus[1]	m	I	n	—	+	—	—	—	—
B. dilatatus	m	I	h	—	+	—	+	+	—
B. peltatus	m	I	h	—	+	+	—	+	—
B. sodalis	b	I	h	—	—	—	—	—	—
B. striatulus V. Hansen	(m)	I?	h	—	—	—	—	—	—
B. unipustulatus	m	I	h (w)	—	—	—	+	—	—
Bembidion aeneum	d	(I)	(h)	—	—	—	—	—	—
B. Andreae polonicum	(m)	I	h	—	+	—	—	+	—
B. argenteolum	m	I	(h)	—	—	—	—	—	—
B. articulatum	m	I	h	—	+	+	—	—	—
B. assimile	d	I	h	—	+	+	—	—	—
B. azurescens	(m)	I	h	—	—	—	—	—	—
B. biguttatum	m	I	h	—	—	—	—	—	—
B. bipunctatum	m	(I)[2]	h	+	+	+	+	+	+
B. Clarki	(d)	I	h (w)	—	—	—	—	—	—
B. dauricum	b	I?	x	—	—	—	—	—	—
B. dentellum	m	I	h	—	—	—	—	—	—
B. difficile	m	I	h	—	—	—	—	—	—
B. Doris	m	I	h	+	+	+	+	+	+
B. femoratum	m	I	(h)	—	—	—	—	—	—
B. fumigatum	m	I	h	—	—	—	—	—	—
B. gilvipes	(d)	I	(h)	—	+	+	+	+	—
B. grapei	(d)	O?	(x)	—	—	+	—	—	—
B. guttula	d	I	h	—	+	+	+	—	—
B. hasti	m	I	h	+	—	—	—	—	—

[1]The subspecies *lacertosus* Sturm has not been omitted here (comp. supplement).

7	8	9	10	11	12	13	14	15	16	17	18	19	20
Värmdön etc.	Ösel and Dagö	Gotska Sandön	Fårön	Gotland	Öland	Bornholm	Ven	Göteborgs Skärgård	Orust	Hvaler	Hitra etc.	Dönna etc.	Lofoten etc.
−	−	−	−	+	+	−	−	−	−	−	−	−	−
−	−	+	+	+	+	+	−	−	−	−	−	−	−
+	−	+	−	+	+	+	−	+	+	−	−	−	+
−	−	+	+	+	+	−	−	−	−	−	−	−	−
+	+	−	−	+	+	−	+	−	−	+	−	−	−
−	−	−	−	+	+	−	−	−	−	−	−	−	−
+	−	+	+	+	+	+	−	−	−	−	−	−	−
+	+	−	+	+	+	+	−	+	+	+	+	−	−
+	−	+	+	+	+	+	−	+	−	−	−	−	+
−	−	+	+	+	+	+	−	−	−	+	−	−	+
+	−	−	−	+	+	+	+	+	−	+	−	−	−
−	+	−	−	−	−	+	−	−	−	−	−	−	−
+	−	+	+	+	+	+	+	+	−	+	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	+	+
+	−	−	+	+	+	+	−	+	+	+	−	−	−
−	+	+	−	+	+	+	+	+	−	−	−	−	−
−	+	−	−	−	−	+	+	−	−	−	−	+	−
+	+	+	+	+	+	+	+	+	+	−	−	−	−
−	−	+	+	+	+	+	−	−	−	+	−	−	−
−	+	+	+	+	+	+	+	−	−	−	−	−	−
−	+	−	−	+	+	+	−	−	−	−	−	−	−
−	−	−	−	−	−	+	−	−	−	−	−	−	−
−	−	−	−	+	+	+	−	−	−	−	−	−	−
−	−	−	−	−	+	−	+	+	+	−	+	+	+
−	+	−	+	−	−	+	+	−	−	−	−	−	−
−	+	−	−	−	−	−	−	−	−	−	−	−	−
+	−	+	−	+	+	+	+	−	−	−	−	−	−
−	+	+	+	+	+	+	+	+	+	+	−	−	−
−	+	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	−	−	+	+	−	−	−	−	−	−
+	+	−	+	+	+	+	−	+	+	+	+	+	+
−	−	−	−	+	+	−	+	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+
−	−	−	−	+	+	+	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+
+	+	+	+	+	+	+	+	−	−	+	−	−	−
−	+	+	−	+	−	−	+	+	−	+	−	−	+
−	−	−	−	−	−	+	−	−	−	−	−	−	−
−	−	−	−	+	+	+	+	+	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+
+	+	+	+	+	+	+	+	+	+	+	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+

	Dynamic group	Hibernation group	Ecological group	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remain-ing outer islands	6 Valamo
Bembidion humerale	(m)	I	(h)	—	+	+	—	—	—
B. illigeri	m	I	h	—	+	—	—	—	—
B. lampros	d	I	n	+	+	+	+	+	+
B. litorale	m	I	(h)	—	—	—	—	—	—
B. lunatum	m	L	h	—	—	—	—	—	—
B. lunulatum	m	I	h	—	—	—	—	—	—
B. minimum	m	I	h	—	+	+	—	—	—
B. nitidulum	m	I	h	—	—	—	—	—	—
B. normannum Dej.	(m)	I?	h	—	—	—	—	—	—
B. obliquum	m	I	h	+	+	+	+	+	+
B. obtusum	d	I	n	—	—	—	—	—	—
B. octomaculatum	m	I	h	—	—	—	—	—	—
B. pallidipenne	m	I	h	—	—	—	—	—	—
B. prasinum	m	I	h	—	—	—	—	—	—
B. properans	(d)	I	n	—	+	+	—	—	—
B. quadrimaculatum	m	I	n	+	+	+	+	+	—
B. quinquestriatum	m	I	n	—	—	—	—	—	—
B. rupestre	m	I	h	+	+	+	+	+	+
B. saxatile	(m)	I	h	—	+	+	+	+	—
B. Schüppeli	(d)	I	h	+	—	—	+	—	—
B. semipunctatum	(m)	I	h	—	—	—	—	—	—
B. Stephensi	m	I	h	—	—	—	—	—	—
B. tenellum Er., Wgn.	(m)	I	h	—	—	—	—	—	—
B. transparens	d	(I)	h	+	+	+	+	+	—
B. unicolor	b	I	(h) (w)	—	+	+	+	—	—
B. ustulatum	d	I	(h)	—	+	—	—	—	—
B. varium	m	I	h	—	+	+	—	—	—
B. velox	m	I	(h)	+	+	—	—	+	+
B virens	(m)	I	h	—	—	—	—	—	—
Blethisa multipunctata	m	I	h	+	+	—	+	+	—
Brachynus crepitans	(m)	(I)	(x)	—	—	—	—	—	—
Bradycellus collaris	d	(I)	n	—	+	—	—	+	—
B. harpalinus	d	(L)	(x)	—	—	—	—	—	—
B. similis	m	I	n	—	—	—	—	—	—
B. verbasci	m	(L)?	(x)	—	—	—	—	—	—
Broscus cephalotes	b	(L)	x	—	+	+	—	—	—
Calathus ambiguus	m	L	(x)	—	+	—	—	—	—
C. erratus	(d)	(L)	(x)	—	+	+	+	+	+
C. fuscipes	b	(L)	n	—	+	+	—	—	—
C. melanocephalus	(d)	(L)	n	+	+	+	+	+	+
C. micropterus	b	(I)	n w	+	+	+	+	—	+
C. mollis	(d)	L	(x)	—	—	—	—	—	—

7 Värmdön etc.	8 Ösel and Dagö	9 Gotska Sandön	10 Fårön	11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.
−	−	−	−	+	−	+	+	−	−	−	−	−	−
+	+	−	−	+	+	+	+	−	−	−	−	−	−
+	+	−	+	+	+	+	+	+	+	+	−	−	−
−	+	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	−	+	−	−	−	−	−	−	−	−
−	−	−	−	−	+	+	+	−	−	−	−	−	−
−	+	+	+	+	+	+	+	−	+	+	−	−	−
−	−	−	−	−	−	+	+	−	−	−	−	−	−
−	−	−	−	−	−	+	−	−	−	−	−	−	−
+	+	+	+	+	+	+	+	+	+	+	−	−	−
−	+	−	+	+	+	+	+	+	−	−	−	−	−
−	−	−	+	−	−	+	−	−	−	−	−	−	−
−	−	+	+	+	+	+	−	−	−	+	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+
−	+	−	+	+	+	−	−	+	+	+	−	−	−
+	+	+	+	+	+	+	+	−	+	+	+	−	−
−	−	−	−	+	+	+	−	−	−	−	−	−	−
+	−	+	+	+	+	+	+	−	+	+	−	+	+
−	+	+	+	+	+	+	+	+	+	+	+	+	+
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−	−	−	−	−	−	+	−	−	−	−	−	−	−
−	−	−	−	−	−	+	+	−	−	−	−	−	−
−	−	−	−	−	−	+	−	−	−	−	−	−	−
−	−	−	+	−	−	+	+	−	−	−	−	−	+
+	−	−	+	+	+	+	+	−	−	−	−	−	−
+	+	−	−	+	+	+	+	+	+	−	−	−	−
−	+	+	+	+	+	+	−	−	−	−	−	−	−
−	+	+	+	+	−	−	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+
−	−	+	+	+	+	+	+	+	−	+	−	+	+
−	−	−	−	+	+	+	−	−	−	−	−	−	−
+	−	+	−	+	+	+	+	−	+	+	−	+	+
−	+	−	+	−	+	−	−	−	−	−	−	−	−
−	−	+	−	−	+	+	−	−	−	−	−	−	−
−	−	−	−	−	−	+	−	−	−	−	−	−	−
−	+	+	+	+	+	+	+	−	−	+	−	−	−
+	+	+	+	+	+	+	+	+	−	+	−	−	−
+	+	+	+	+	+	+	−	+	+	+	−	−	−
+	+	+	+	+	+	+	+	+	+	+	+	−	−
+	+	+	+	+	+	+	−	+	+	+	+	+	+
+	+	+	+	+	+	+	−	−	+	+	+	−	+
−	−	+	−	+	+	+	+	−	−	−	−	−	−

	Dynamic group	Hibernation group	Ecological group	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remaining outer islands	6 Valamo
Calosoma auropunctatum	m	I	n	—	—	—	—	—	—
C. inquisitor	m	I	n w	—	—	—	—	—	—
C. investigator	(m)	I?	(x)?	—	—	—	—	—	—
C. reticulatum	(m)	I	x	—	—	—	—	—	—
C. sycophanta	m	I	n w	—	—	—	—	—	—
Carabus arvensis	b	I	(x)	—	—	—	—	—	—
C. cancellatus	b	I	n	—	—	—	—	—	—
C. clathratus	d	(I)	h	+	+	+	—	+	—
C. convexus	b	I	(x)	—	—	+	—	—	—
C. coriaceus	b	(L)	n w	—	—	—	—	—	—
C. glabratus	b	(L)	n (w)	—	—	—	—	—	+
C. granulatus	b	I	(h)	+	+	—	+	+	+
C. hortensis	b	L	n	+	+	+	+	—	—
C. intricatus	b	I	n w	—	—	—	—	—	—
C. nemoralis	b	I	n	—	+	—	—	—	—
C. nitens	b	I	n	+	+	+	—	+	—
C. problematicus	b	O	x	—	—	—	+	—	—
C. violaceus	b	(L)	n (w)	—	+	+	—	—	—
Chlaenius nigricornis	m	I	h	—	+	+	—	—	—
C. nitidulus SCHRK.	(m)	I	h	—	—	—	—	—	—
C. quadrisulcatus	m	I	(h)	—	—	—	—	—	—
C. sulcicollis	m	I	h	—	—	—	—	—	—
C. tristis	m	I	h	—	+	—	+	—	—
C. vestitus	(m)	I	h	—	—	—	—	—	—
Cicindela campestris	m	O	(x)	—	+	+	—	+	—
C. hybrida	m	O	x	—	—	—	—	+	+
C. maritima	m	O	x	+	—	—	—	+	—
C. silvatica	m	O	x	+	+	+	+	+	+
Clivina fossor	m	I	n	+	+	+	+	+	—
Cychrus caraboides	b	(L)	n (w)	—	+	+	+	—	+
Cymindis angularis	b	(L)	x	—	+	+	—	+	—
C. humeralis	b	(L)	x	—	—	—	—	—	—
C. macularis	(d)	L	x	+	+	+	+	—	—
C. vaporariorum	d	(L)	(x)	—	—	+	+	—	—
Demetrias imperialis	m	I	h	—	—	—	—	—	—
D. monostigma	b	I	n	—	—	—	—	—	—
Dichirotrichus pubescens	m	L	(h)	—	—	—	—	—	—
Dolichus halensis	m	L	n	—	—	—	—	—	—
Dromius agilis	m	(I)	a	—	+	+	+	+	—
D. angustus	m	(I)	a	—	—	—	—	—	—
D. fenestratus	m	I	a	—	+	+	—	+	—
D. linearis	(d)	(I)	x	—	+	+	—	—	—

7 Värmdön etc.	8 Ösel and Dagö	9 Gotska Sandön	10 Fårön	11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.
—	—	—	—	—	+	—	—	—	—	—	—	—	—
+	+	—	—	—	+	—	—	—	—	—	—	—	—
—	—	—	—	—	+	—	—	—	—	—	—	—	—
—	—	—	—	—	+	—	—	—	—	—	—	—	—
—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	+	—	—	—	—	+	—	—	—	—	—	—	—
—	+	—	—	—	+	+	—	+	+	+	—	—	—
—	+	—	+	—	+	—	—	+	—	—	—	—	—
—	+	—	—	—	—	—	—	—	—	—	—	—	—
—	+	—	—	—	+	+	—	—	—	—	+	—	—
—	+	—	—	+	+	—	—	—	—	—	+	+	+
—	+	—	+	+	+	+	—	+	+	+	—	—	—
+	+	—	—	+	+	+	—	—	+	+	+	+	—
—	—	—	—	—	—	+	—	—	—	—	—	—	—
+	+	—	+	+	+	+	+	—	+	+	+	—	—
—	+	—	+	+	+	+	—	+	—	+	—	+	—
+	—	—	—	—	—	—	—	+	—	+	+	—	+
+	—	—	+	+	+	+	—	—	—	—	+	+	+
—	+	—	+	+	+	+	—	+	—	+	—	—	—
—	—	—	—	—	—	+	—	—	—	—	—	—	—
—	—	—	—	—	+	—	—	—	—	—	—	—	—
—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	+	—	+	+	+	—	—	—	+	—	—	—
—	—	—	—	—	—	+	—	—	—	—	—	—	—
+	+	—	+	+	+	+	—	+	+	+	—	+	—
—	—	—	—	—	—	+	+	—	+	—	—	—	—
—	+	—	—	—	—	+	—	—	—	—	—	—	—
—	+	+	+	+	+	+	—	+	—	+	—	—	—
+	+	—	—	+	+	+	+	+	+	—	+	+	+
+	+	+	—	+	+	+	—	—	+	—	+	+	+
—	—	—	+	+	+	+	—	+	—	+	—	—	—
—	—	—	—	+	+	+	—	—	—	—	—	—	—
—	—	—	+	—	+	+	—	—	—	+	—	—	—
—	+	—	—	—	+	+	—	+	—	—	+	—	+
—	—	—	+	—	—	—	—	—	—	—	—	—	—
—	—	—	—	+	+	—	—	—	—	—	—	—	—
—	—	—	—	+	+	—	—	+	+	+	+	+	+
—	—	—	—	—	—	+	+	—	—	—	—	—	—
+	—	—	+	+	+	+	—	—	—	+	—	—	—
—	—	+	—	+	—	+	—	—	—	—	—	—	—
—	—	+	—	+	+	+	—	—	+	+	—	—	—
+	—	—	+	+	+	+	+	—	—	—	—	—	—

	Dynamic group	Hibernation group	Ecological group	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remaining outer islands	6 Valamo
Dromius longiceps	m	I	n	+	—	—	—	—	—
D. marginellus	m	I	a	—	+	+	+	—	—
D. melanocephalus	(m)	I	(x)	—	—	—	—	—	—
D. nigriventris	(d)	I	(x)	—	+	+	—	—	—
D. quadraticollis	m	I	a	—	—	—	—	+	—
D. quadrimaculatus	m	I	a	—	+	+	—	—	—
D. quadrinotatus	m	I	a	—	—	+	—	—	—
D. sigma	(d)	I	(h)	+	+	+	—	—	—
Dyschirius aeneus	m	I	h	—	+	+	—	—	—
D. angustatus	(m)	I	(h)	—	—	—	—	—	—
D. globosus	b	I	(h)	+	+	+	+	+	—
D. impunctipennis	m	I	h	—	+	—	—	—	—
D. intermedius	(m)	I	(h)	—	—	—	—	—	—
D. lüdersi	m	I	h	+	+	+	—	—	—
D. obscurus	m	I	h	+	—	—	—	+	—
D. politus	m	I	(h)	—	+	—	—	+	—
D. salinus	(m)	I	h	—	+	+	—	—	—
D. septentrionum	(m)	I	h	—	—	—	—	—	—
D. thoracicus	m	I	h	+	+	+	—	+	+
Elaphrus cupreus	m	I	h	+	+	+	—	+	+
E. lapponicus	(m)	I	h	—	—	—	—	—	—
E. riparius	m	I	h	+	+	—	+	+	+
E. uliginosus	(m)	I	h	—	+	+	+	—	—
Harpalus aeneus	m	I	(x)	+	+	+	+	+	+
H. anxius	m	I	x	—	—	—	—	—	—
H. azureus	d	(I)	x	—	—	—	—	—	—
H. calceatus	m	L	x	—	—	—	—	+	—
H. distinguendus	m	I	x	—	—	—	—	—	—
H. frölichi	m	I	x	—	—	—	—	—	—
H. fuliginosus	(m)	I	(x)	—	—	—	—	—	—
H. griseus	m	(L)	x	—	—	—	—	+	—
H. hirtipes	m	(I)	x	—	—	—	—	—	—
H. latus	m	O	n	+	+	+	+	+	+
H. luteicornis	(m)	I	n	—	—	+	—	—	—
H. melancholicus	(m)	(L)	x	—	—	—	—	—	—
H. melleti	m	(I)	(x)	—	—	—	—	—	—
H. neglectus	(d)	I	x	—	—	—	—	—	—
H. picipennis	d	I	x	—	—	—	—	—	—
H. pubescens	m	(L)	n	—	+	+	+	+	+
H. punctatulus	m	O	(x)	—	—	+	—	—	—
H. puncticeps	(m)	(L)	(x)	—	—	—	—	—	—
H. puncticollis	(m)	I	x	—	+	—	—	—	—

7 Värmdön etc.	8 Ösel and Dagö	9 Gotska Sandön	10 Fårön	11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	+	+	+	—	—	—	—	—	—	—
—	—	—	—	—	—	+	+	—	—	—	—	—	—
—	+	+	+	+	+	+	—	+	+	+	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	+	—	—	+	+	+	—	—	+	+	—	—	—
+	+	+	+	+	+	+	—	—	—	+	+	—	—
—	—	—	—	+	—	+	—	—	—	—	—	—	—
—	—	+	+	+	+	—	+	—	—	—	—	—	—
—	—	—	—	—	—	—	+	—	—	—	—	—	—
+	+	—	+	+	+	+	+	+	+	+	+	+	+
—	—	+	+	—	+	+	—	—	—	—	—	—	—
—	—	—	—	—	—	—	+	—	—	—	—	—	—
—	+	+	+	+	+	+	+	+	—	—	—	—	—
—	+	—	+	+	+	+	—	—	+	—	—	—	—
—	—	—	+	+	+	—	+	—	—	—	—	—	—
—	+	—	—	+	—	—	—	+	—	+	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	+	—
—	+	—	+	+	+	+	+	+	+	+	—	—	—
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+	+	—	+	+	+	+	—	—	+	—	+	+	—
+	+	+	—	+	+	—	—	—	—	+	+	—	—
+	+	+	+	+	+	+	+	+	+	+	+	—	—
—	—	—	—	+	+	+	—	—	—	—	—	—	—
—	—	—	+	+	+	+	—	—	—	—	—	—	—
+	—	+	+	—	+	+	—	—	—	—	—	—	—
+	+	—	—	—	—	+	—	—	—	—	—	—	—
—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	—	—	—	+	+	—	—	—	+	—	—	—
—	—	+	+	+	+	+	—	—	—	—	—	—	—
—	—	—	—	+	+	+	—	—	—	—	—	—	—
+	+	—	+	+	+	+	+	+	+	+	+	+	—
—	—	—	+	+	—	—	—	+	—	—	—	—	—
—	—	—	—	+	+	+	—	—	—	—	—	—	—
—	—	—	+	+	+	+	+	—	—	—	—	—	—
—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	—	—	—	+	—	—	—	—	—	—	—	—
+	+	+	+	+	+	+	+	+	+	—	—	—	—
—	+	+	—	+	+	—	—	—	—	—	—	—	—
—	—	—	—	—	+	+	+	—	—	—	—	—	—
+	+	—	—	—	+	—	—	—	—	—	—	—	—

	Dynamic group	Hibernation group	Ecological group	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remaining outer islands	6 Valamo
Harpalus quadripunctatus	(m)	O	n (w)	—	+	—	+	+	—
H. rubripes	m	O	(x)	—	+	—	—	—	—
H. rufitarsis	m	I	x	—	—	—	—	—	—
H. rufus	(m)	(L)	x	—	—	—	—	—	—
H. rupicola	m	I	(x)	—	—	—	—	—	—
H. seladon	m	I	n	—	+	+	+	—	—
H. serripes	m	I	x	—	—	—	—	—	—
H. servus	(m)	I	x	—	—	—	—	—	—
H. signaticornis DFT.	(m)	I	(x) ?	—	—	—	—	—	—
H. smaragdinus	m	(L)	x	—	+	—	—	—	—
H. tardus	m	(I)	(x)	—	+	—	—	—	—
H. vernalis	b	(I)	x	—	—	—	—	—	—
H. winkleri	m	I	n	—	+	—	—	—	—
Lebia chlorocephala	m	(I)	n	—	+	+	—	—	+
L. crux-minor	m	I	n	—	+	+	—	—	—
L. cyanocephala	m	I	(x)	—	+	+	—	—	—
Leistus ferrugineus	b	L	n	—	+	+	+	—	+
L. rufescens	b	L	h (w)	—	+	—	+	—	+
L. ruformarginatus	(m)	L	n w	—	—	—	—	—	—
Licinus depressus	b	I	x	—	+	+	—	—	—
Loricera pilicornis	m	(I)	h	+	+	+	+	+	—
Masoreus wetterhalli	(d)	(L)	x	—	—	—	—	—	—
Metabletus foveatus	b	I	x	—	+	—	—	—	—
M. truncatellus	d	I	(x)	—	+	+	+	—	+
Microlestes maurus	(d)	I	(x)	—	—	—	—	—	—
M. minutulus	m	I	(x)	—	+	+	—	+	—
Miscodera arctica	m	I	(x)	—	+	—	+	—	—
Nebria brevicollis	m	(L)	n	—	+	—	—	—	—
N. gyllenhali	(m)	(L)	h	—	+	—	+	—	+
N. livida	(m)	L	h	—	—	—	+	—	—
N. salina	(m)	(L)	(x)	—	—	—	—	—	—
Notiophilus aquaticus	d	O	n	+	+	+	—	+	—
N. biguttatus	(d)	I	n (w)	+	+	+	+	—	+
N. germinyi	(d)	L	(x)	—	+	+	—	—	+
N. palustris	(d)	I	n	—	+	+	+	—	+
N. pusillus	(m)	(L)	(x)	—	+	—	—	—	—
Odacantha melanura	(m)	I	h	—	+	—	—	—	—
Olisthopus rotundatus	(d)	(L)	(x)	—	+	+	—	—	—
Omophron limbatum	m	O	h	—	—	—	—	—	—
Oodes helopioides	m	I	h	—	+	—	—	—	—
Panagaeus bispustulatus	(m)	I	(x)	—	—	+	—	—	—
P. crux-major	(m)	I	h	—	+	—	+	—	—

7 Värmdön etc.	8 Ösel and Dagö	9 Gotska Sandön	10 Fårön	11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.
+	—	+	—	+	+	+	—	+	+	+	—	—	+
+	—	+	+	+	+	+	+	—	+	—	—	—	—
—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	—	—	—	+	+	—	—	—	—	—	—	—
—	—	—	—	+	+	+	—	—	—	—	—	—	—
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+	+	+	+	+	+	+	—	+	+	—	—	—	—
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+	+	+	+	+	+	+	+	+	+	+	+	+	+
+	+	—	—	—	+	+	—	—	+	—	—	—	—
—	—	—	—	—	—	+	—	—	—	—	—	—	—
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—	+	+	+	+	+	+	+	—	+	+	+	+	+
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+	—	—	—	—	+	+	+	+	—	+	—	—	—
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+	+	+	+	+	+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	—	—	+	+	+	+
+	+	+	+	+	+	—	+	+	+	+	—	+	+
+	+	—	+	+	+	+	+	—	+	—	—	—	—
+	+	—	+	+	+	+	—	+	+	+	—	—	—
—	+	—	+	+	+	—	—	—	—	+	—	—	—
+	+	—	+	+	+	+	—	+	+	—	—	—	—
—	—	—	—	—	—	+	+	—	—	—	—	—	—
—	+	—	—	+	+	+	—	—	—	—	—	—	—
—	+	—	+	+	+	+	—	—	—	—	—	—	—
+	+	—	+	+	+	+	+	—	—	—	—	—	—

	Dynamic group	Hibernation group	Ecological group	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remaining outer islands	6 Valamo
Patrobus assimilis	b	(L)[2]	n	+	+	+	—	—	+
P. atrorufus	b	(L)	n	—	+	+	+	—	+
P. septentrionis	m	O	h	—	—	—	—	—	—
P. septentrionis australis	(m)	L?	h	—	—	—	—	—	+
Pelophila borealis	m	I	h	—	—	—	—	—	—
Pristonychus terricola	b	O	k	—	—	+	—	—	—
Pterostichus adstrictus	m	I	n	+	—	—	—	—	—
P. angustatus	(m)	I	(x)	—	+	—	—	—	—
P. anthracinus	d	I	h	—	—	—	—	—	—
P. aterrimus	m	I	h	—	—	—	+	+	—
P. coerulescens	m	I	n	—	+	+	—	—	+
P. cupreus	m	I	n	—	+	+	+	—	+
P. diligens	(d)	(I)	h	—	+	+	+	+	+
P. gracilis	m	(I)	h	—	+	—	—	—	—
P. lepidus	(d)	L	x	+	—	—	—	+	—
P. minor	(d)	(I)	h	—	+	+	+	+	+
P. niger	m	(L)	n	—	+	+	+	+	+
P. nigrita	m	(I)	h	+	+	+	+	+	+
P. oblongopunctatus	(m)	(I)	n w	+	+	+	+	+	+
P. punctulatus	(m)	I	x	—	—	—	—	—	—
P. strenuus	d	I	(h)	+	+	+	+	+	—
P. vernalis	(d)	I	(h)	—	+	+	+	+	—
P. vulgaris	(d)	(L)	n	—	+	+	+	+	+
Sphodrus leucophthalmus	m	L	k	—	—	—	—	—	—
Stenolophus mixtus	m	I	h	—	—	—	—	+	—
S. skrimshiranus Steph.	(m)	I	h	—	—	—	—	—	—
S. teutonus	(m)	I	(h)	—	—	—	—	—	—
Stomis pumicatus	b	I	n	—	—	—	—	—	—
Synuchus nivalis	(d)	L	(x)	—	+	+	—	+	+
Tachyta nana	(m)	I	a	—	—	—	—	—	+
Trechus discus	m	L	n	—	+	+	—	—	—
T. fulvus	b	L?	h	—	—	—	—	—	—
T. obtusus	b	(L)	n	—	—	—	—	—	—
T. quadristriatus	m	L	(x)	—	+	+	—	+	—
T. rivularis	(d)	L	h w	—	—	—	—	—	+
T. rubens	m	(I)	(h)	+	+	+	+	—	+
T. secalis	b	L	n (w)	+	+	+	+	—	—
Trichocellus cognatus	m	I	(x)	+	—	—	—	—	—
T. placidus	(m)	I	n (w)	+	+	+	+	+	—
Zabrus tenebrioides	m	L	n	—	—	—	—	—	—
Total species				53	157	124	87	77	59

7 Värmdön etc.	8 Ösel and Dagö	9 Gotska Sandön	10 Fårön	11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.
+	−	−	+	+	−	−	−	−	−	−	+	+	+
+	+	−	+	+	+	+	+	−	+	+	−	+	+
−	−	−	−	−	−	−	−	−	−	−	−	+	+
−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	+	−	−	+
−	+	−	−	−	+	+	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	+	+
−	−	−	−	−	−	+	−	−	−	−	−	−	−
−	+	+	−	+	+	+	−	−	−	−	−	−	−
−	−	−	−	+	+	+	−	+	−	−	−	−	−
+	+	+	+	+	+	+	+	−	+	+	−	−	−
+	+	−	−	+	+	+	−	−	+	+	−	−	−
+	−	−	+	+	+	+	+	+	+	+	+	+	+
−	−	+	−	+	+	+	−	−	−	−	−	−	−
−	+	−	−	+	+	+	−	−	−	+	−	−	−
+	−	−	−	+	+	+	+	+	+	+	+	−	−
+	+	+	+	+	+	+	+	+	+	+	+	+	−
+	+	−	+	+	+	+	+	+	+	+	+	+	+
+	+	+	−	+	+	+	−	+	+	+	+	−	+
−	−	−	−	+	+	+	−	−	−	−	−	−	−
+	−	−	+	+	+	+	+	+	+	+	+	+	+
−	+	−	+	+	+	+	+	+	+	+	−	−	−
+	+	−	+	+	+	+	+	+	+	+	−	−	−
−	+	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	−	+	+	−	−	−	−	−	−	−
−	−	−	−	−	−	+	−	−	−	−	−	−	−
−	−	−	−	−	−	+	−	−	−	−	−	−	−
−	+	−	−	+	+	+	−	−	−	−	−	−	−
+	+	+	+	+	+	+	+	−	+	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	−	−	−	+	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	+	−	−
−	−	−	+	+	+	+	−	−	−	−	+	−	+
+	+	+	+	+	+	+	+	+	+	+	−	−	−
+	−	−	−	−	−	−	−	−	−	−	−	−	−
−	+	−	−	+	+	−	−	−	−	−	−	+	+
+	+	−	+	+	+	+	+	−	+	+	+	−	−
−	−	−	−	+	+	−	−	−	−	−	−	+	+
+	−	+	+	+	+	+	+	−	−	+	−	−	+
−	−	−	−	−	−	+	−	−	−	−	−	−	−
104	131	90	134	195	221	226	104	87	87	107	49	46	64

Table 10. Comparison of dynamic groups of carabid species of islands and of the mainland. Cf. explanation with Table 9

Last three columns give percentage deviation of insular faunas from those of mainland regions compared.

	m	(m)	d	(d)	b	Percentage deviation from region of comparison		
	Species %	Species %	Species %	Species %	Species %	m+(m)	d + (d)	b
1. Hailuoto	31 = 58,5	4 = 7,5	4 = 7,6	7 = 13,2	7 = 13,2	— 0,4	— 1,0	+ 1,4
Region of comparison	61 = 51,3	18 = 15,1	7 = 5,9	19 = 15,9	14 = 11,8			
2. Åland	89 = 56,7	20 = 12,7	10 = 6,4	19 = 12,1	19 = 12,1	— 0,2	+ 1,25	— 1,05
Region of comparison a	103 = 54,5	28 = 14,8	10 = 5,3	22 = 11,6	26 = 13,8			
,, b	94 = 53,4	29 = 16,5	8 = 4,5	23 = 13,1	22 = 12,5			
3. Ålands Skärgård	65 = 52,4	12 = 9,7	10 = 8,1	20 = 16,1	17 = 13,7	— 7,8	+ 6,6	+ 1,2
Region of comparison	94 = 53,4	29 = 16,5	8 = 4,5	23 = 13,1	22 = 12,5			
4. Hogland	46 = 52,9	12 = 13,8	6 = 6,9	12 = 13,8	11 = 12,6	— 3,35	+ 4,5	— 1,15
Region of comparison a	82 = 55,8	19 = 12,9	7 = 4,8	18 = 12,2	21 = 14,3			
,, b	124 = 53,0	43 = 18,4	11 = 4,7	25 = 10,7	31 = 13,2			
5. Remaining outer islands	48 = 62,3	9 = 11,7	6 = 7,8	10 = 13,0	4 = 5,2	+ 3,25	+ 4,95	— 8,2
Region of comparison a	112 = 52,3	38 = 17,8	9 = 4,2	26 = 12,1	29 = 13,6			
,, b	124 = 53,0	43 = 18,4	11 = 4,7	25 = 10,7	31 = 13,2			
6. Valamo	30 = 50,8	8 = 13,6	2 = 3,4	11 = 18,6	8 = 13,6	— 7,4	+ 5,0	+ 2,4
Region of comparison	100 = 53,2	35 = 18,6	8 = 4,2	24 = 12,8	21 = 11,2			
7. Värmdön	55 = 52,8	12 = 11,6	6 = 5,8	15 = 14,4	16 = 15,4	— 3,7	+ 2,7	+ 1,0
Region of comparison	99 = 51,9	29 = 15,2	11 = 5,8	22 = 11,7	27 = 14,4			
8. Ösel and Dagö	69 = 52,6	13 = 10,0	11 = 8,4	16 = 12,2	22 = 16,8	— 8,25	+ 5,7	+ 2,55
Region of comparison a	124 = 53,0	43 = 18,4	11 = 4,7	25 = 10,7	31 = 13,2			
,, b	113 = 52,6	38 = 17,7	11 = 5,1	20 = 9,3	33 = 15,3			
9. Gotska Sandön	61 = 67,7	9 = 10,0	6 = 6,7	8 = 8,9	6 = 6,7	+ 8,95	— 0,35	— 8,6
Region of comparison a	99 = 54,1	24 = 13,1	11 = 6,0	21 = 11,5	28 = 15,3			
,, b	113 = 52,6	38 = 17,7	11 = 5,1	20 = 9,3	33 = 15,3			
10. Fårön	71 = 53,0	17 = 12,7	12 = 9,0	18 = 13,4	16 = 11,9	— 3,05	+ 6,45	— 3,4
Region of comparison a	99 = 54,1	24 = 13,1	11 = 6,0	21 = 11,5	28 = 15,3			
,, b	113 = 52,6	38 = 17,7	11 = 5,1	20 = 9,3	33 = 15,3			
11. Gotland	106 = 54,4	30 = 15,4	12 = 6,1	23 = 11,8	24 = 12,3	+ 0,9	+ 1,25	— 2,15
Region of comparison a	109 = 52,9	30 = 14,6	12 = 5,8	27 = 13,1	28 = 13,6			
,, b	113 = 52,6	38 = 17,7	11 = 5,1	20 = 9,3	33 = 15,3			
12. Öland	118 = 53,4	33 = 14,9	17 = 7,7	25 = 11,3	28 = 12,7	— 0,4	+ 2,4	— 2,0
Region of comparison a	111 = 52,1	32 = 15,0	12 = 5,6	28 = 13,2	30 = 14,1			
,, b	113 = 52,6	38 = 17,7	11 = 5,1	20 = 9,3	33 = 15,3			
13. Bornholm	122 = 54,0	39 = 17,2	14 = 6,2	23 = 10,2	28 = 12,4	+ 0,5	+ 0,4	— 0,9
Region of comparison	138 = 52,5	48 = 18,2	12 = 4,6	30 = 11,4	35 = 13,3			

	m	(m)	d	(d)	b	Percentage deviation from region of comparison		
	Species %	Species %	Species %	Species %	Species %	m+(m)	d + (d)	b
14. Ven	**58=55,8**	**13=12,5**	**10= 9,6**	**14=13,5**	**9= 8,6**	— **2,95**	+ **7,45**	— **4,5**
Region of comparison a	140=52,4	50=18,7	11= 4,1	30=11,3	36=13,5			
,, b	128=50,8	52=20,6	11= 4,4	29=11,5	32=12,7			
15. Göteborgs Skärgård	**46=52,0**	**10=11,5**	**11=12,6**	**11=12,6**	**9=10,4**	— **4,5**	+ **7,1**	— **2,6**
Region of comparison	115=53,2	34=15,7	11= 5,1	28=13,0	28=13,0			
16. Orust	**45=51,8**	**6= 6,9**	**10=11,5**	**13=14,9**	**13=14,9**	—**10,3**	+ **8,6**	+ **1,7**
Region of comparison	115=52,5	36=16,5	11= 5,0	28=12,8	29=13,2			
17. Hvaler	**56=52,4**	**15=14,0**	**8= 7,5**	**13=12,1**	**15=14,0**	— **1,7**	+ **3,4**	— **1,7**
Region of comparison	104=52,8	30=15,3	10= 5,1	22=11,1	31=15,7			
18. Hitra & c.	**19=38,7**	**4= 8,2**	**4= 8,2**	**5=10,2**	**17=34,7**	—**19,1**	+ **0,9**	+**18,2**
Region of comparison	55=50,4	17=15,6	5= 4,6	14=12,9	18=16,5			
19. Dönna & c.	**23=50,0**	**4= 8,7**	**4= 8,7**	**6=13,0**	**9=19,6**	— **9,2**	+ **5,7**	+ **3,5**
Region of comparison	40=49,4	15=18,5	4= 4,9	9=11,1	13=16,1			
20. Lofoten, Vesterålen	**29=45,3**	**11=17,2**	**6= 9,4**	**7=10,9**	**11=17,1**	— **8,2**	+ **4,3**	+ **3,8**
Region of comparison	34=45,3	19=25,4	3= 4,0	9=12,0	10=13,3			

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Table 11. Insular specimens of dimorphic species examined

m—Macropterous specimens; b—Brachypterous specimens; + —Recorded on the island but material not available

	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remaining outer islands	6 Valamo	7 Värmdö etc.	9 Gotska Sandön	10 Fårön
Agonum fuliginosum	—	4 b	2 b	2 b	1 b	1 b	19 b	—	+
A. moestum	—	—	1 m	—	—	—	—	—	1 m
A. obscurum	—	1 m 2 b	3 b	—	—	—	18 b	—	2 b
Amara infima	—	—	—	—	—	—	—	—	—
Bembidion aeneum	—	—	—	—	—	—	—	—	—
B. assimile	—	2 b	2 m 3 b	—	—	—	—	1 m	4 m
B. clarki	—	—	—	—	—	—	—	—	—
B. gilvipes	—	2 b	1 b	2 m	1 m	—	—	—	—
B. grapei	—	—	1 m	—	—	—	—	—	—
B. guttula	—	5 m 6 b	1 m 3 b	2 m	—	—	1 m 2 b	3 m	7 m
B. lampros	1 b	2 m 6 b	4 b	3 m	1 m 1 b	1 b	1 m 6 b	—	2 b
B. obtusum	—	—	—	—	—	—	—	—	4 m
B. properans	—	7 b	10 b	—	—	—	—	—	1 b
B. schüppeli	1 b	—	—	1 b	—	—	—	—	—
B. transparens	2 b	1 m 2 b	1 m 7 b	2 m	1 m	—	—	—	3 m
B. ustulatum	—	2 b	—	—	—	—	2 b	—	—
Bradycellus collaris	—	1 b	—	—	1 m	—	13 b	2 m 1 b	—
B. harpalinus	—	—	—	—	—	—	—	—	2 m
Calathus erratus	—	10 m 4 b	4 m 1 b	2 m 3 b	1 m 4 b	+	10 m 9 b	11 b	7 b
C. melanocephalus	1 b	4 b	7 b	1 b	1 m	1 b	8 b	2 m 3 b	9 b
C. mollis	—	—	—	—	—	—	—	10 m	—
Carabus elathratus	1 b	3 b	1 b	—	+	—	—	—	1 b
Cymindis macularis	1 b	3 b	2 b	3 m	—	—	—	—	2 b
C. vaporariorum	—	—	1 b	1 m	—	—	—	—	—
Dromius linearis	—	2 b	10 b	—	—	—	4 b	—	2 b
D. nigriventris	—	3 b	29 b	—	—	—	—	6 m 2 b	1 b
D. sigma	1 b	4 b	8 b	—	—	—	—	—	—
Harpalus azureus	—	—	—	—	—	—	—	—	3 m
H. neglectus	—	—	—	—	—	—	—	—	—
H. picipennis	—	—	—	—	—	—	—	—	—
Masoreus wetterhalli	—	—	—	—	—	—	—	1 b	1 m 3 b
Metabletus truncatellus	—	6 b	9 b	3 b	—	1 b	5 b	5 b	1 m 6 b
Microlestes maurus	—	—	—	—	—	—	—	—	1 b
Notiophilus aquaticus	2 b	11 b	8 b	—	1 b	—	2 m 5 b	1 b	4 b

11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.	Tromsö	Mageröy
4 b	2 b	7 b	—	—	—	—	+	3 b	1 b	—	—
1 m 14 b	5 m 9 b	9 m	—	—	1 m	1 m	—	—	—	—	—
1 m 10 b	8 b	35 b	+	—	1 b	6 b	—	—	—	—	—
—	6 b	3 b	—	—	—	—	—	—	—	—	—
—	34 m	—	1 m 2 b	1 m 1 b	1 m	—	2 b	1 b	1 b	—	—
57 m 1 b	7 m 3 b	8 m	3 m	5 b	3 b	9 b	—	—	—	—	—
13 b	2 m 4 b	—	1 m	—	—	—	—	—	—	—	—
1 m 28 b	3 m 3 b	+	1 m	+	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	1 m 4 b	—	—
5 m 10 b	5 m 3 b	1 m 2 b	5 m 1 b	5 b	+	+	—	—	—	—	—
1 m 21 b	28 m 4 b	10 b	3 m 4 b	2 b	1 m 9 b	+	—	—	—	—	—
5 m 13 b	8 m 10 b	2 m 5 b	1 m 8 b	2 b	—	—	—	—	—	—	—
2 m. 6 b	14 b	—	—	3 b	4 b	11 b	—	—	—	—	—
—	—	—	—	—	—	—	—	4 b	1 b	—	—
—	—	1 m	1 m	—	—	—	—	—	+	—	—
34 b	3 b	4 b	6 b	2 b	3 b	—	—	—	—	—	—
5 b	3 m 6 b	2 b	1 b	—	1 m	4 m	—	1 b	8 b	—	—
—	4 m	—	—	—	—	—	—	—	—	—	—
1 m 10 b	1 m 39 b	4 b	—	6 b	1 m	3 b	—	—	—	—	—
25 b	9 b	4 b	—	2 b	4 b	1 b	1 b	5 b	8 b	4 b	1 b
3 m 15 b	25 m 47 b	24 m 7 b	1 b	—	—	—	—	—	—	—	—
—	3 b	—	—	10 b	—	—	—	—	—	—	—
—	13 b	10 b	—	—	—	7 b	—	—	—	—	—
—	1 b	+	—	5 b	—	—	+	—	1 b	+	—
1 m 5 b	10 b	10 b	13 b	—	—	—	—	—	—	—	—
12 b	3 b	4 b	—	6 b	+	4 b	—	—	—	—	—
7 b	—	+	—	—	—	—	—	—	—	—	—
44 m 104 b	86 b	10 b	—	—	—	—	—	—	—	—	—
—	25 m 2 b	11 b	—	—	—	—	—	—	—	—	—
—	2 m 3 b	—	—	—	—	—	—	—	—	—	—
3 b	20 b	10 b	—	—	—	—	—	—	—	—	—
1 m 11 b	6 b	+	—	7 b	2 b	1 m 3 b	—	—	—	—	—
4 m 16 b	13 b	1 b	1 b	—	—	—	—	—	—	—	—
3 m 13 b	11 m 2 b	3 b	1 m	6 b	2 b	6 b	+	1 b	8 b	5 b	7 b

	1 Hailuoto	2 Åland	3 Ålands Skärgård	4 Hogland	5 Remaining outer islands	6 Valamo	7 Värmdö etc.	9 Gotska Sandön	10 Fårön
Notiophilus biguttatus	2 m	3 m 2 b	1 m	2 m	—	1 b	1 m 3 b	3 m	+
N. germinyi	—	2 b	1 b	—	—	3 b	6 b	8 b	4 b
N. palustris	—	2 b	3 b	2 m 1 b	—	1 b	10 b	—	1 m
Olisthopus rotundatus	—	3 m 25 b	1 m	—	—	—	5 m 30 b	—	7 b
Pterostichus anthracinus	—	—	—	—	—	—	—	1 m	—
P. diligens	—	9 b	3 b	1 b	5 b	1 b	10 b	—	1 m
P. lepidus	3 b	—	—	—	2 b	—	—	—	—
P. minor	—	10 b	1 b	5 m 2 b	1 m	1 m	2 b	—	—
P. strenuus	—	6 b	3 b	1 b	1 b	—	3 b	—	5 b
P. vernalis	1 m 1 b	1 m 4 b	3 m 2 b	2 m 1 b	3 m 2 b	—	—	—	1 b
P. vulgaris	—	4 b	1 m 2 b	1 b	1 m 2 b	1 b	2 b	—	2 b
Synuchus nivalis	—	3 m 1 b	1 b	—	1 m	1 b	1 m 5 b	1 m	1 m 1 b
Trechus rivularis	—	—	—	—	—	1 b	2 m 22 b	—	—

11 Gotland	12 Öland	13 Bornholm	14 Ven	15 Göteborgs Skärgård	16 Orust	17 Hvaler	18 Hitra etc.	19 Dönna etc.	20 Lofoten etc.	Tromsö	Mageröy
10 m 6 b	4 m 1 b	18 m 7 b	1 m 1 b	—	—	2 m 2 b	1 b	1 b	22 b	1 m 7 b	1 b
15 b	5 b	—	1 b	5 b	6 b	1 b	—	1 b	4 b	1 b	—
8 b	3 m 8 b	1 m 6 b	2 b	—	1 m	—	—	—	—	—	—
1 m 13 b	1 m 12 b	4 m 24 b	—	5 b	1 b	—	—	—	—	—	—
23 b	5 m 40 b	1 m 3 b	—	—	—	—	—	—	—	—	—
1 m 13 b	7 b	3 m 20 b	2 b	1 b	+	1 m 2 b	2 b	3 b	3 b	36 b	—
11 b	2 b	5 b	—	—	—	1 b	—	—	—	—	—
1 m 35 b	1 m 3 b	4 m 20 b	1 m	9 b	2 b	10 b	1 m	—	—	—	—
35 b	1 m 2 b	17 b	1 b	1 b	2 b	4 b	4 b	4 b	36 b	—	—
12 b	1 m 3 b	3 b	1 m	4 b	1 b	1 b	—	—	—	—	—
7 b	2 b	20 b	1 b	1 b	2 b	+	—	—	—	—	—
2 m 2 b	3 m 1 b	2 m 2 b	1 b	—	1 m 7 b	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—

228 **Table 12. Comparison between dynamic groups in insular and mainland faunas after separating dimorphic species (see Table 11)**

d—Dimorphic on island or in mainland region; d?—Species for which no material was available (ignored in calculating percentages). Ösel and Dagö could not be taken into consideration. Numbers for mainland regions (= regions of comparison) are largely based only on calculations. Last two columns give percentage deviation of insular faunas from those of respective mainland regions

	m + (m)	d	b	d?	Percentage deviation from region of comparison	
	Species %	Species %	Species %	Species	b	b + d
1. Hailuoto	36 = 67,9	1 = 1,9	16 = 30,2	—	+6,9	+0,5
Region of comparison	82 = 68,4	10 = 8,3	28 = 23,3			
2. Åland	109 = 69,4	8 = 5,1	40 = 25,5	—	+4,3	+0,7
Region of comparison a	132 = 69,5	18 = 9,5	40 = 21,0			
” b	124 = 70,8	15 = 8,6	36 = 20,6			
3. Ålands Skärgård	81 = 65,3	6 = 4,9	37 = 29,8	—	+9,2	+5,5
Region of comparison	124 = 70,8	15 = 8,6	36 = 20,6			
4. Hogland	65 = 74,7	4 = 4,6	18 = 20,7	—	+0,5	−4,3
Region of comparison a	101 = 68,7	15 = 10,2	31 = 21,1			
” b	168 = 71,5	21 = 8,9	46 = 19,6			
5. Remaining outer islands	63 = 82,9	4 = 5,3	9 = 11,8	1	−8,3	−11,4
Region of comparison a	153 = 71,5	17 = 7,9	44 = 20,6			
” b	168 = 71,5	21 = 8,9	46 = 19,6			
6. Valamo	39 = 67,2	0	19 = 32,8	1	+15,7	+7,1
Region of comparison	139 = 74,3	16 = 8,6	32 = 17,1			
7. Värmdön	67 = 64,4	8 = 7,7	29 = 27,9	—	+6,7	+4,4
Region of comparison	130 = 68,8	19 = 10,0	40 = 21,2			
9. Gotska Sandön	76 = 84,5	3 = 3,3	11 = 12,2	—	−8,8	−15,6
Region of comparison a	125 = 67,9	20 = 10,9	39 = 21,2			
” b	151 = 69,9	20 = 9,3	45 = 20,8			
10. Fårön	97 = 73,5	3 = 2,3	32 = 24,2	2	+3,2	−4,6
Region of comparison a	125 = 67,9	20 = 10,9	39 = 21,2			
” b	151 = 69,9	20 = 9,3	45 = 20,8			
11. Gotland	136 = 69,8	20 = 10,2	39 = 20,0	—	−1,0	−0,7
Region of comparison a	142 = 68,3	22 = 10,6	44 = 21,1			
” b	151 = 69,9	20 = 9,3	45 = 20,8			
12. Öland	153 = 69,2	21 = 9,5	47 = 21,3	—	+0,2	−0,1
Region of comparison a	147 = 68,4	22 = 10,2	46 = 21,4			
” b	151 = 69,9	20 = 9,3	45 = 20,8			

	m + (m)	d	b	d?	Percentage deviation from region of comparison	
	Species %	Species %	Species %	Species	b	b + d
13. Bornholm	**164 = 72,9**	**10 = 4,4**	**51 = 22,7**	1	+3,4	**−2,0**
Region of comparison	188 = 70,9	26 = 9,8	51 = 19,3			
14. Ven	**79 = 76,7**	**5 = 4,9**	**19 = 18,4**	1	−0,75	**−5,4**
Region of comparison a	191 = 71,0	28 = 10,4	50 = 18,6			
” b	182 = 71,6	22 = 8,7	50 = 19,7			
15. Göteborgs Skärgård	**56 = 65,1**	**1 = 1,2**	**29 = 33,7**	1	+14,4	**+ 5,1**
Region of comparison	153 = 70,2	23 = 10,5	42 = 19,3			
16. Orust	**56 = 65,1**	**2 = 2,3**	**28 = 32,6**	1	+13,6	**+5,0**
Region of comparison	155 = 70,1	24 = 10,9	42 = 19,0			
17. Hvaler	**73 = 68,9**	**4 = 3,8**	**29 = 27,3**	1	+ 5,5	**+0,1**
Region of comparison	136 = 69,0	18 = 9,2	43 = 21,8			
18. Hitra & c.	**24 = 49,0**	**0**	**25 = 51,0**	—	+23,5	**+19,8**
Region of comparison	75 = 68,8	4 = 3,7	30 = 27,5			
19. Dönna & c	**27 = 58,7**	**0**	**19 = 41,3**	—	+12,9	**+9,2**
Region of comparison	55 = 67,9	3 = 3,7	23 = 28,4			
20. Lofoten, Vesterålen	**39 = 60,9**	**1 = 1,6**	**24 = 37,5**	—	+14,5	**+ 11,1**
Region of comparison	54 = 72,0	3 = 4,0	18 = 24,0			

Note: Following dimorphic species are denoted “b” (brachypterous), although no material was available: *Agonum fuliginosum* (from Hitra), *Bembidion transparens* (from Lofoten), *Cyminidis vaporariorum* (from Bornholm, Hitra), *Dromius nigriventris* (from Orust), *D. signa* (from Bornholm), *Metabletus truncatellus* (from Bornholm), *Notiophilus aquaticus* (from Hitra), *Pterostichus diligens* (from Orust), *P. vulgaris* (from Hvaler). *Bembidion lampros* from Hvaler is denoted “d” (dimorphic).

230 **Table 13. Comparison between flightless and dimorphic species (b and d, Table 12) of islands and mainland (= regions of comparison according to hibernation type (O, L, I, etc., Table 9)**

Ösel and Dagö omitted.

b—Constantly brachypterous species; b(d)—Dimorphic species, but brachypterous in region of study; d—Constantly dimorphic species, including region of study.

Last column: Index of deviation from fauna of mainland district compared.

	A. Larval hibernators O + L + (L)				B. Imago hibernators I + (I)				Index A:B	Percentage deviation from region of comparison
	b	b (d)	d	Total	b	b (d)	d	Total		
1. Hailuoto	**3**	**4**	**0**	**7**	**4**	**5**	**1**	**10**	**0,70**	**—0,03**
Region of comparison	8	5	3	16	6	9	7	22	0,73	
2. Åland	**11**	**5**	**4**	**20**	**8**	**16**	**5**	**29**	**0,69**	**—0,14**
Region of comparison a	14	4	7	25	10	10	11	31	0,81	
,, b	12	6	5	23	9	8	10	27	0,85	
3. Ålands Skärgård	**10**	**7**	**2**	**19**	**6**	**14**	**2**	**22**	**0,86**	**+0,01**
Region of comparison	12	6	5	23	9	8	10	27	0,85	
4. Hogland	**7**	**2**	**1**	**10**	**4**	**5**	**3**	**12**	**0,83**	**+0,14**
Region of comparison a	10	4	5	19	10	6	10	26	0,73	
,, b	12	6	7	25	15	9	14	38	0,66	
5. Remaining outer islands	**1**	**2**	**2**	**5**	**3**	**4**	**1**	**8**	**0,63**	**—0,03**
Region of comparison a	13	5	6	24	15	10	11	36	0,67	
,, b	12	6	7	25	15	9	14	38	0,66	
6. Valamo	**6**	**5**	**0**	**11**	**2**	**6**	**0**	**8**	**1,38**	**+0,75**
Region of comparison	10	4	5	19	12	7	11	30	0,63	
7. Värmdön	**10**	**4**	**5**	**19**	**6**	**10**	**2**	**18**	**1,06**	**+0,28**
Region of comparison	14	3	8	25	11	10	11	32	0,78	
9. Gotska Sandön	**4**	**4**	**1**	**9**	**2**	**1**	**2**	**5**	**1,80**	**+1,12**
Region of comparison a	14	4	7	25	12	7	13	32	0,78	
,, b	11	5	6	22	17	7	14	38	0,58	
,, b										
10. Fårön	**9**	**8**	**2**	**19**	**7**	**8**	**1**	**16**	**1,19**	**+0,51**
Region of comparison a	14	4	7	25	12	7	13	32	0,78	
,, b	11	5	6	22	17	7	14	38	0,58	
11. Gotland	**13**	**5**	**6**	**24**	**11**	**11**	**13**	**35**	**0,69**	**+0,01**
Region of comparison a	14	7	7	28	12	9	15	36	0,78	
,, b	11	5	6	22	17	7	14	38	0,58	
12. Öland	**14**	**8**	**5**	**27**	**13**	**12**	**15**	**40**	**0,68**	**+0,01**
Region of comparison a	14	7	7	28	13	9	15	37	0,76	
,, b	11	5	6	22	17	7	14	38	0,58	
13. Bornholm	**13**	**9**	**3**	**25**	**14**	**14**	**7**	**35**	**0,71**	**+0,01**
Region of comparison	16	6	9	31	17	10	17	44	0,70	

	A. Larval hibernators O + L + (L)				B. Imago hibernators I + (I)				Index A : B	Percentage deviation from region of comparison
	b	b (d)	d	Total	b	b (d)	d	Total		
14. Ven	**5**	**4**	**0**	**9**	**4**	**7**	**5**	**16**	**0,56**	**—0,17**
Region of comparison a	17	4	11	32	17	10	17	44	0,73	
” b	15	7	7	29	16	9	15	40	0,73	
15. Göteborgs Skärgård	**4**	**7**	**0**	**11**	**5**	**13**	**1**	**19**	**0,58**	**—0,10**
Region of comparison	14	5	7	26	13	9	16	38	0,68	
16. Orust	**7**	**6**	**1**	**14**	**6**	**9**	**1**	**16**	**0,88**	**+0,20**
Region of comparison	14	4	8	26	13	9	16	38	0,68	
17. Hvaler	**8**	**8**	**0**	**16**	**7**	**6**	**4**	**17**	**0,94**	**+0,15**
Region of comparison	15	4	7	26	14	8	11	33	0,79	
18. Hitra & c.	**12**	**4**	**0**	**16**	**4**	**5**	**0**	**9**	**1,78**	**+0,24**
Region of comparison	13	4	3	20	4	8	1	13	1,54	
19. Dönna & c.	**7**	**3**	**0**	**10**	**2**	**7**	**0**	**9**	**1,11**	**—0,25**
Region of comparison	10	3	2	15	3	7	1	11	1,36	
20. Lofoten, Vesterålen	**8**	**4**	**1**	**13**	**2**	**7**	**1**	**10**	**1,30**	**—0,33**
Region of comparison	8	3	2	13	3	4	1	8	1,63	

Note: *Bembidion dauricum* and *Pristonychus terricola* omitted. Hibernation type of former is not known. *Pristonychus* is certainly introduced all over.

232 **Table 14. Ecological grouping of flightless and dimorphic species (b and d, Table 12) of islands and the respective mainland (= regions of comparison).**

See explanation with Table 9. Ösel and Dagö omitted.
Last two columns give percentage deviation from fauna of mainland district compared.

	x	(x)	n	(h)	h	w	(w)	Percentage deviation from region of comparison	
	Species %	Species %	Species %	Species %	Species %	Species %	Species %	x+(x)	w+(w)
1. Hailuoto	**2=11,8**	**0**	**8=47,1**	**4=23,5**	**3=17,6**	**1=5,9**	**1= 5,9**	— 6,7	—14,5
Region of comparison	2= 5,3	5=13,2	15=39,5	8=21,0	8=21,0	2=5,3	8=21,0		
2. Åland	**6=12,5**	**6=12,5**	**19=39,6**	**8=16,7**	**9=18,7**	**1=2,1**	**8=16,7**	+ 1,2	— 4,0
Region of comparison a	7=12,5	7=12,5	22=39,3	9=16,1	11=19,6	3=5,4	9=16,1		
,, b	6=12,2	5=10,2	21=42,9	9=18,4	8=16,3	3=6,1	9=18,4		
3. Ålands Skärgård	**5=12,2**	**7=17,1**	**15=36,5**	**7=17,1**	**7=17,1**	**1=2,4**	**6=14,6**	+ 6,8	— 7,5
Region of comparison	6=12,3	5=10,2	21=42,8	9=18,4	8=16,3	3=6,1	9=18,4		
4. Hogland	**1= 4,6**	**2= 9,1**	**9=40,9**	**5=22,7**	**5=22,7**	**1=4,6**	**5=22,7**	—11,6	+ 7,5
Region of comparison a	3= 6,5	6=13,0	20=43,5	9=19,6	8=17,4	2=4,3	8=17,4		
,, b	8=12,3	11=16,9	22=33,9	10=15,4	14=21,5	3=4,6	9=13,8		
5. Other outer islands	**2=15,4**	**1= 7,7**	**4=30,75**	**4=30,75**	**2=15,4**	**0**	**1= 7,7**	— 3,3	—13,1
Region of comparison a	6=10,0	8=13,3	24=40,0	10=91,7	12=20,0	5=8,3	9=15,0		
,, b	8=12,3	11=16,9	22=33,9	10=15,4	14=21,5	3=4,6	9=13,8		
6. Valamo	**0**	**3=15,8**	**11=57,9**	**1= 5,3**	**4=21,0**	**1=5,3**	**5=26,3**	— 0,5	+11,2
Region of comparison	3= 6,1	5=10,2	19=38,8	9=18,4	13=26,5	2=4,1	8=16,3		
7. Värmdön	**4=10,8**	**5=13,5**	**17=46,0**	**4=10,8**	**7=18,9**	**1=2,7**	**8=21,6**	— 2,0	+ 3,2
Region of comparison	7=12,3	8=14,0	22=38,6	8=14,0	12=21,1	3=5,3	9=15,8		
9. Gotska Sandön	**3=21,4**	**4=28,6**	**7=50,0**	**0**	**0**	**1=7,1**	**1= 7,1**	+21,8	— 5,4
Region of comparison a	6=10,5	8=14,0	23=40,4	9=15,8	11=19,3	3=5,3	9=15,8		
,, b	10=16,7	9=15,0	21=35,0	8=13,3	12=20,0	3=5,0	8=13,3		
10. Fårön	**6=17,1**	**7=20,0**	**15=42,9**	**5=14,3**	**2= 5,7**	**1=2,9**	**4=11,4**	+ 9,0	— 5,4
Region of comparison a	6=10,5	8=14,0	23=40,4	9=15,8	11=19,3	3=5,3	9=15,8		
,, b	10=16,7	9=15,0	21=35,0	8=13,3	12=20,0	3=5,0	8=13,3		
11. Gotland	**9=15,3**	**8=13,5**	**24=40,6**	**9=15,3**	**9=15,3**	**1=1,7**	**7=11,9**	— 3,4	— 4,1
Region of comparison a	11=17,2	10=15,6	23=35,9	9=14,1	11=17,2	2=3,1	9=14,1		
,, b	10=16,7	9=15,0	21=35,0	8=13,3	12=20,0	3=5,0	8=13,3		
12. Öland	**13=19,4**	**10=14,9**	**25=37,3**	**9=13,5**	**10=14,9**	**2=3,0**	**9=13,5**	+ 2,3	— 1,2
Region of comparison a	11=16,9	10=15,4	24=36,9	9=13,9	11=16,9	2=3,1	9=13,9		
,, b	10=16,7	9=15,0	21=35,0	8=13,3	12=20,0	3=5,0	8=13,3		
13. Bornholm	**13=21,3**	**9=14,8**	**23=37,7**	**8=13,1**	**8=13,1**	**3=4,9**	**9=14,8**	+ 2,8	+ 2,4
Region of comparison	13=17,3	12=16,0	27=36,0	10=13,4	13=17,3	4=5,3	9=12,0		

	x	(x)	n	(h)	h	w	(w)	Percentage deviation from region of comparison	
	Species %	Species %	Species %	Species %	Species %	Species %	Species %	x+(x)	w+(w)
14. Ven	**3=12,0**	**4=16,0**	**11=44,0**	**5=20,0**	**2= 8,0**	**0**	**3=12,0**	**— 4,2**	**— 6,5**
Region of comparison a	13=17,1	12=15,8	27=35,5	11=14,5	13=17,1	5=6,6	9=11,8		
” b	11=15,7	11=15,7	26=37,2	11=15,7	11=15,7	4=5,7	9=12,9		
15. Göteborgs Skärgård	**3=10,0**	**6=20,0**	**10=33,3**	**6=20,0**	**5=16,7**	**0**	**0**	**— 1,2**	**—17,2**
Region of comparison	10=15,6	10=15,6	24=37,6	10=15,6	10=15,6	2=3,1	9=14,1		
16. Orust	**0**	**5=16,7**	**14=46,6**	**5=16,7**	**6=20,0**	**1=3,3**	**5=16,7**	**—13,0**	**+ 1,2**
Region of comparison	9=14,1	10=15,6	24=37,5	10=15,6	11=17,2	3=4,7	9=14,1		
17. Hvaler	**6=18,2**	**4=12,1**	**14=42,5**	**4=12,1**	**5=15,1**	**1=3,0**	**4=12,1**	**+ 4,0**	**— 7,7**
Region of comparison	6=10,5	9=15,8	22=38,6	11=19,3	9=15,8	4=7,0	9=15,8		
18. Hitra & c.	**1= 4,0**	**1= 4,0**	**15=60,0**	**4=16,0**	**4=16,0**	**2=8,0**	**5=20,0**	**—10,2**	**+ 0,7**
Region of comparison	2= 6,1	4=12,1	18=54,5	5=15,2	4=12,1	2=6,1	7=21,2		
19. Dönna & c.	**0**	**1= 5,3**	**12=63,1**	**3=15,8**	**3=15,8**	**0**	**5=26,3**	**— 6,3**	**— 8,3**
Region of comparison	0	3=11,6	16=61,5	4=15,4	3=11,5	2=7,7	7=26,9		
20. Lofoten	**2= 8,3**	**3=12,5**	**12=50,0**	**3=12,5**	**4=16,7**	**1=4,2**	**5=20,8**	**+ 6,5**	**— 8,4**
Region of comparison	0	3=14,3	11=52,4	3=14,3	4=19,0	1=4,8	6=28,6		

Note: *Pristonychus terricola* is not taken into consideration.

53 species, that of the mainland region of comparison, 119 species. In view of the far greater surface of the latter, the inevitable impoverishment of the fauna is rather less than expected. This is largely attributable to the striking variety of biotopes in Hailuoto. The missing species, according to present knowledge, belong to no particular dynamic group (Tables 10, 12) or group based on a developmental stage (Table 13). With regard to ecology (Table 14) the most striking feature is under-representation of the xerophilous species, but especially of forest species. Nevertheless, it may be concluded that Hailuoto represents a remarkable example of *how an island can be colonized in a relatively short period (< 2000 years) by a fauna completely "normal" in composition.*

236 This cannot be explained solely by the overall development of biotopes on the island: *the possibilities of immigration* must have been exceptionally favorable. It is not easy to decide whether the main reason was the short distance from the mainland or the formerly busy shipping. The assumption of an anthropochorous dispersal is *contradicted* by the fact that only two species

found in Hailuoto (*Dromius longiceps* and *Dyschirius lüdersi*) seem to be absent from the mainland (= region of comparison), in spite of the active shipping contact which apparently occurred earlier between distant localities in the southern part. It is difficult to attribute the formation of a fauna, which is "normal" in all respects, to anthropochorous dispersal as the most important factor.

The rapid and uniform colonization of Hailuoto by the fauna is in my view due to its short distance from the mainland, and to the fact that a big river, the Ule, empties in its immediate vicinity. During spate in spring this river brings enormous quantities of various alluvial material into the sea. Especially at this time of year, when drift ice is also brought down by the river, all kinds of objects lying on the ice or frozen into it, such as tree trunks, twigs, reeds, soil, etc. can be transported far out to sea. Successful landing of such transported objects at Hailuoto, lying only 27 km from the mouth of the river, might take place every year. —Comparison with the islands of the Province Oa (Replot, Björkö, etc.) situated in Kvarken, which are about the same age (Valovirta, 1937, p. 35 ff.) and are similarly isolated but lack such favorable location close to a river mouth, would undoubtedly be highly informative. Unfortunately their coleopteran fauna is imperfectly known.

2. Åland

We will consider here only the main island (Swedish "Fasta Åland") and Eckerö which is separated from it by the narrow Marsund. The Skärgård farther east has faunistic peculiarities and is best treated separately.

Fasta Åland is an extremely fragmented island with an area of 937 km^2 (including Eckerö), which has developed gradually by the joining of small islands rising out of the sea (see map in Hausen, 1910a) and is continuously growing in size. The highest point, Orrdalsklint in Saltvik, is at an altitude of 132 m above sea level. The present rate of land emergence varies around 5 mm per year (Witting, 1943, p. 28; Hausen, 1946, p. 82). The oldest known
237 culture ("Gånggrift" period) corresponds to a location on the shoreline at 34 to 36 m above sea level, with a maximum age of 5000 years (Hausen, 1910a, p. 56; Munthe, 1940, pp. 189, 201, Plate XV). The highest points in Åland may have risen from the sea as naked rocky skerries as late as the Ancylus period, perhaps around 7000 BC (Munthe, l.c., Plate XI; Sauramo, 1942, p. 240).

The nearest distance to the mainland, Väddö in Upl, is 38 km (from Eckerö). The nearest point on the Finnish mainland (Ab Taivassalo) is 76 km away, and Estonia is a good 200 km away.

The population is about 20,000 persons, a remarkable density, which gives the island the striking appearance of a cultivated landscape. There are active trade connections with both Sweden and the Finnish mainland. In earlier times these were predominantly through Stockholm, but since the political separation from Sweden (in 1809) mainly through Åbo.

Åland has an exceedingly high variety of biotopes (cf. the summary in Swedish by A. Palmgren, 1943–44, p. 20 ff.). Particularly striking are the luxuriant meadows of leaves (= "Laubwiesen") and groves (A. Palmgren, 1915 to 1917); otherwise coniferous forest is dominant. The numerous lakes belong to diverse types (Cedercreutz, 1937), likewise the seashores. In Eckerö even quicksand is found (Krogerus, 1929). The mountainous terrain consists almost without exception of granite (Hausen, 1946, p. 31).

The large number of species of the *flora* (vascular plants) in Åland is very striking (650 "large species"; A. Palmgren, 1925, p. 44), which even surpasses that of the corresponding region on the South Finnish mainland (l.c., p. 54). —Unfortunately there is no comprehensive account of the *beetle fauna* of Åland but it is possible to extract an almost complete list of species from the *Catalogus* (1939). The two contributions by Håk. Lindberg (1924, 1925) are only reports of collecting. Most records are unpublished and are only represented by specimens in museums and private collections.

The *carabid fauna*, according to our present knowledge, comprising 157 species is strikingly rich, though not to the same extent as the flora. In the number of species it is of course surpassed not only by the region of comparison in Uppland (with 189 species) but also by that of the Finnish mainland (with 176 species). The composition of the fauna on the basis of dynamic groups is fairly normal; the preponderance of dimorphic species (Table 10, "d + [d]") and functionally brachypterous species (Table 12, "b + d") is small, i.e. only
238 two and one species respectively. More striking is the deficit of species that hibernate in the larval stage (Table 13, last column). Ecologically (Table 14) there is a small preponderance of xerophilous species (x + [x]) and a larger deficit of forest species (w + [w]).

The origin as well as the time, direction and mode of immigration of the flora and fauna of Åland present a series of captivating problems on which much has already been written. The recent origin of the island and its location almost midway between two areas of mainland which during the postglacial period obtained their fauna largely independent of one another from different directions, render the questioning extremely concrete.

A. Palmgren, in a series of contributions, dealt thoroughly with the immigration of the flora to Åland, and in 1927 summarized his results. After a detailed comparison with the flora of neighboring regions (Upl; Ab, Nl; Estonia) he concluded that "a predominant part of the flora of Åland has been received from Sweden. The immigration from Finland has seemingly been very slight. Immigration from the eastern Baltic was stronger, though scarcely significant" (1927, p. 79). He bases this idea mainly on the gradual reduction in the number of species within the landscape limits of Åland from west to east. The reason is "the increasing distance to the east from a center of dispersal in

the west (in Sweden)†. . ." (1921, p. 71). On this Palmgren bases his postulate on "the distance as a phytogeographical factor."

A detailed and effective criticism of this point of view was provided by Eklund (1931, pp. 71–92). In the Skärgård of Åboland (Korpo and Houtskär) he found a similar reduction, especially in the flora of leaf meadows (="Laubwiesen"), which there diminishes from north to south and is clearly due to *edaphic* factors. He concludes that the reduction in the number of species in the landscape of Åland toward the east is due to the *decrease in limestone in the same direction.*

It is moreover really astonishing that Palmgren bases a "theory of distance" exclusively on statistical grounds without considering the dispersal ecology of the plants. It would have been natural to attempt a division of the species into anemochorous, hydrochorous, etc., whence his "theory" might have received causal confirmation. But even in his comprehensive contribution "The routes of immigration of the flora to the islands of Åland†" (1927), in which each of
239 over 50 species is treated separately in detail, no data at all are provided on the nature and mode of dispersal of the diaspores.

On the other hand Eklund (1931, pp. 88 ff.) devoted special attention to the dynamics of plants and in particular dealt with the possibilities of hydrochorous passive dispersal (also experimentally; 1927a, 1927b, 1929). He summarized his conclusions on the routes of immigration (1931, pp. 105–106) as follows: 1. "A large main immigration of the flora from Sweden to Åland and in general to the Finnish rocky skerries may not have taken place." 2. ". . . an immigration from the south (i.e. from the eastern Baltics) seems far more significant than earlier assumed." Palmén (1944, pp. 224 ff.) accepted this interpretation with regard to insects, and went somewhat too far in ascribing to Eklund a greater role of the 'Baltic' immigration route than he actually proposed (see quote).

Let us examine to what extent the carabid fauna of Åland can contribute to a solution of these questions. It includes a number of species, although small, for which the immigration route seems more or less clear, solely with regard to their distribution on the mainland (see maps in Part II).

Swedish origin may therefore be assumed for the following 12 species:

Agonum lugens
Badister bipustulatus s. str. (see Supplement)
Bembidion illigeri
Calathus fuscipes
Dormius linearis
D. nigriventris
Harpalus winkleri
Licinus depressus
Metabletus foveatus
Nebria brevicollis
Odacantha melanura
Olisthopus rotundatus.

†(Original German quotation translated into English; suppl. scient. edit.).

With the exception of *Licinus, Olisthopus* and possibly the form of *Badister*, as far as is known they are absent from the northern coast of Estonia and from Dagö (altogether 3 or 4 of them are found in Estonia; *Harpalus winkleri* uncertain). On the Finnish mainland *Agonum* and *Nebria* are completely absent and possibly the form of *Badister*; *Bembidion* and *Dromius linearis* appear to occur there as more or less accidental immigrants. The rest were found only as rarities in the southwestern corner (certainly immigrated from Åland) (*Metabletus* and *Calathus* also in the extreme southeast) with the exception of *Harpalus*, which is unknown in Ab. The immigration route of *Olisthopus* is clarified (p. 373) by the map showing wing-dimorphic forms (Fig. 32; p. 373).

240 An *eastern* origin, from the Finnish mainland (F) or from the Baltics (B), can be assumed for the following 11 Åland species:

Acupalpus exiguus F
A. flavicollis B
Amara majuscula F?
Bembidion andreae polonicum B
B. humerale F
B. minimum B?
B. varium B?
Cymindis macularis F
Dyschirius impunctipennis B?
D. salinus B
Microlestes minutulus F?

A distinction between a southeastern ("Baltic") and a purely eastern immigration from the Finnish mainland is especially difficult in cases where southwestern Finland also apparently received its stock of the species in question from the Baltics (but possibly at earlier times), as in the case of *Bembidion minimum* and *B. varium*. However, in the present context it is only of minor importance since the intention was to present a group for comparison with the above "Swedish" group. —*Amara majuscula* might also occur in Estonia (although confused with *apricaria*). *Dyschirius impunctipennis* may have immigrated from Gotska Sandön or Fårön, as assumed by Krogerus for the ecologically corresponding species *Bledius tibialis* Heer. All 11 species are either missing from the parts of the Swedish mainland (Sdm, Upl) lying opposite (e.g. *Bembidion andreae, Cymindis, Dyschirius impunctipennis, D. salinus, Microlestes*) or are found there very rarely, more or less sporadically (e.g. *Acupalpus flavicollis, Bembidion humerale, B. minimum, B. varium*), or have evidently immigrated very late (e.g. *Acupalpus exiguus, Amara majuscula*; cf. pp. 622 ff.).

Do the members of these two groups of immigrants in the fauna of Åland show any basic differences? A division based on ecology (Tables 9, 14) reveals the following:

	"Swedish group"	"Eastern group"
xerophilous [x, (x)]	5 species	2 species
mesophilous (n)	4 species	1 species
hygrophilous [h, (h)]	3 species	8 species

In the "eastern" group, therefore, the hygrophilous species predominate. Since the same group includes 5 species (the species of *Bembidion* and *Dyschirius*, with the exception of *B. humerale*) which always lead a littoral existence (along the sea) it is natural to consider hydrochorous transport from the
241 Baltics (cf. Eklund, 1931, pp. 93 ff.). However, the 5 species mentioned are all capable of steady flight, and so could use anemohydrochorous transport (in Palemén's sense, 1944). The idea is strongly supported by the fact that 7 of the 11 species of the "eastern" group (all, with the exception of *Bembidion andreae*, *cymindis*, and species of *Dyschirius*) were found in his drift material (1944, pp. 37–39).

This brings us to a more important difference between the two groups treated here, which is evident from the following division according to the *dynamics* of the species (Tables 9, 10):

	"Swedish group"	"Eastern group"
macropterous [m, (m)]	6 species	10 species
dimorphic [d, (d)]	3 species	1 species
brachypterous (b)	3 species	0 species

Table 11 shows that 3 of the 4 dimorphic Åland species are found exclusively in the brachypterous form and the fourth (*Olisthopus*) predominantly so.

A comparison with the entire fauna of Åland is best carried out according to the division in Table 12:

	m + (m)	d	b	b + d percentage deviation
The entire fauna of Åland	109 species = 69%	8 species = 5%	40 species =26%	
"Swedish group"	6 species = 50%	1 species = 8%	5 species = 42%	+19
"Eastern group"	10 species = 91%	0	1 species = 9%	−21

The "Swedish group" in the fauna of Åland thus includes a large part for which anemochorous dispersal can scarcely be considered.

For a closer acquaintance with this western group, and following Palmgren's "distance principle," I also analyzed the dynamics of the species that occur on Åland exclusively in Eckerö (the western part). These are given below:

**Acupalpus exiguus*	*A. dolens*
Agonum assimile	*A. quadripunctatum*

Amara ingenua
**A. majuscula*
242 *A. municipalis*
A. ovata
Badister dilatatus
**Bembidion andreae polonicum*
B. gilvipes
**B. humerale*
Bradycellus collaris
Carabus granulatus
C. nemoralis
Chlaenius nigricornis
**Cymindis macularis*
Dromius marginellus
Dyschirius aeneus
**D. impunctipennis*
Notiophilus pusillus
Pterostichus gracilis

It is amazing to find that six of these species (asterisk) belong to the "eastern" group treated above. This agrees with Eklund's idea (1931, pp. 88, 96), according to which at least the hydrochorously dispersed plant disseminules have "far greater prospects of even reaching western Åland from the eastern Baltics than from Sweden." Although there is hardly any purely hydrochorous dispersal of the beetles in question, their distribution shows that Palmgren's "distance theory" is not applicable even to organisms independent of limestone, i.e.: *The distribution of carabids within the confines of Åland does not provide any adequate clues to their immigration route.*

Therefore I proceeded to examine and consider *the entire coleopteran fauna*, the species *found in Finland* (borders prior to the Second World War) *exclusively in the landscape Åland* (Al, also including the Skärgård of Åland). The material was obtained from the *Catalogus* (1939), from further references in "Notulae Ent." and "Ann. Ent. Fenn.", and from Mr. Hellén and Mr. Anton Jansson (Table 15). The records from the eastern Baltics were taken from the relevant literature.

244 Of the 42 species in Table 15, which could not have immigrated to Åland from the mainland of Finland, 30 are found in east-central Sweden and 28 in Upl. As far as is known, 22 of the species in question are native to the eastern Baltic.

Thus immigration from parts of Sweden next to Åland is inconceivable or at any rate most improbable for at least 12 species, 3 of which (*Bagous, Diphyllus, Limnobaris*) are nevertheless found northward up to Ögl. —*Bledius tibialis*, unknown in the eastern Baltics, may have come from Gotska Sandön, as proposed by Krogerus (1929, p. 72), and possibly *Drilus* from Gotland (p. 248).

As far as is known, therefore, no fewer than 20 of the 42 species are absent from the eastern Baltics and another 6 from Estonia; in Ösel and Dagö altogether only 11 species are found. Nevertheless, a small component of the eastern Baltic element in the group is quite natural, considering the poor exploration of these regions. Had their members arrived in Åland from the Baltics, it would have been very strange if they had not simultaneously colonized the mainland of southwestern Finland. With the exception of the 12 species mentioned they may be considered as some of the most definite

representatives of the *Swedish* element in the coleopteran fauna of Åland.

We now proceed to an opposite group: *those species of Åland province* (also including the Skärgård of Åland), *that are not found in east-central Sweden* (Table 16).

246 The list of 83 species is quite impressive, especially when compared with the 42 species in Table 15. The two lists are not directly comparable: in the first case we are dealing with the species of Åland entirely absent from Finland, in the second only those absent from east-central Sweden. But the great role played by eastern or southeastern immigration of the coleopteran fauna of Åland is clearly evident. Eleven species ("p" in list) are represented in Palmén's drift material.

Eleven species (*Airaphilus*, *Apion pisi*, *Bledius tibialis*, *Brachygluta*, *Cassida*, *Ceuthorrhynchus schönherri*, *Diphyllus*, *Drilus*, *Limnobaris*, *Stenus lindbergi*, *Trogophloeus nitidus*) are common to both lists; they may have arrived from the south (or the southeast). Moreover, it is striking that out of the second list (Table 16) only 3 species (*Chromoderus, Heterocerus obsoletus, Triarthron*) are missing from southwestern Finland (Ab, Nl, St, Ta), and also (with the exception of *Chromoderus*) as far as is known, from the Baltics, where many of the remaining species are also unknown. *The most important immigration route of the Coleoptera to Åland might have been from the east, from the Finnish mainland.*

To return to the point where we felt obliged to extend the discussion to the entire coleopteran fauna, we have the question of the *modes of dispersal* of the beetles that immigrated to Åland. It is seen from an examination of the "non-carabids" in the two lists above that they are fully winged almost without exception*, i.e. they have in all probability immigrated in the *anemochorous* (or *anemohydrochorous*) mode. Exceptions are: in the "Swedish" group (Table 15, excluding the common species of both lists) *Chrysomela haemoptera, Galeruca laticollis*, and *Lycoperdian succincta***; in the "eastern" group (Table 16
248 excluding the common species) *Eonius* and *Scleropterus*. From among the "common" species only *Drilus* (female) must have immigrated from the south (or from the southeast).

The last species (as larva and female) lives as a parasite in the shells of *Helix*, and therefore must have extraordinary opportunities to be transported hydrochorously with the host over long distances (possibly as impregnated

*I have not examined all the species in Tables 15 and 16 regarding the formation of the hind wings but only those which on the basis of their mode of life (soil insects!) could be presumed flightless. The following "suspected" species turned out to be *macropterous*: *Anthicus umbrinus*, *Apion pisi*, *Brachygluta helferi*, *Chromoderus fasciatus*, *Oxypoda brachyptera*, *Reichenbachia impressa*, *Stenus scabriculus*, *Tachyporus tersus.*

**West (1940–41, p. 391) erroneously considered *Lycoperdina succincta* as capable of flight. Two specimens from Denmark (Asserbo Overdrev) and from Ögl (Mogata) show completely rudimentary wings.

 Table 15. Coleoptera (except Carabidae) of Al province (Åland) not found elsewhere in Finland

b—Brachypterous; d—Dimorphic

	Upl	Upl Sdm Vst Nke	Gtl	Ösel Dagö	Est-land	Ost-baltikum
Agabus chalconotus PANZ.	+	+	+	+	+	+
Agathidium varians BECK	+	+	—	—	—	—
Airaphilus perangustus HAR. LINDB	—	—	—	—	—	—
Aphodius contaminatus HBST.	—	+	+	—	—	—
Apion pisi FBR.	—	—	+	+	+	+
Bagous brevitarsis V. HANSEN	—	—	—	—	—	—
Bledius tibialis HEER	—	—	+	—	—	—
Brachygluta helferi SCHM.-GOEB.	—	—	—	—	—	—
Cassida stigmatica SUFFR.	—	—	—	—	—	—
Ceuthorrhynchus pollinarius FORST.	+	+	+	—	—	+
C. schönherri BRIS.	—	—	+	—	—	—
b Chrysomela haemoptera L [1]	+	+	+	+	+	+
Coccidula scutellata HBST	+	+	—	—	—	—
Coeliodes ruber MRSH.	+	+	—	—	—	—
Cryptophagus affinis STURM	+	+	+	—	—	+
C. populi PAYK.	+	+	+	—	+	+
Cteniopus flavus SCOP.	+	+	+	—	—	+
Dasytes coeruleus DE G.	+	+	+	+	+	+
Dermestes laniarius ILL.	+	+	+	+	+	+
Diphyllus lunatus FBR	—	—	—	—	—	—
♀*b Drilus concolor* AHR.	—	—	+	+	+	+
b Galeruca laticollis SAHLB. [2]	+	+	—	—	—	+
Graphoderes cinereus L.	+	+	—	—	+	+
Graptodytes bilineatus STURM	+	+	+	—	+	+
Gymnetron pascuorum GYLL.	+	+	+	+	+	+
Hedobia imperialis L.	+	+	+	+	+	+
Hypocyptus suecicus PALM	+	+	—	—	—	—
Laccobius striatulus FBR.	+	+	+	+	+	+
Limnobaris reitteri MUNST.	—	—	—	—	+	+
Liodes curta FAIRM.	—	+	+	—	—	—
Lissodema cursor GYLL.	+	+	—	—	—	—
b Lycoperdina succincta L.	+	+	+	—	—	+
Micropeplus fulvus ER.	+	+	+	—	—	—
Octotemnus mandibularis GYLL.	+	+	—	—	—	—
Oedemera croceicollis GYLL.	+	+	—	—	—	—
Olibrus bicolor FBR.	+	+	+	+	+	+
Reichenbachia impressa PANZ.	+	+	—	—	—	+
Silis ruficollis FBR.	+	+	—	—	—	—
(*d*) *Sitona humeralis* STEPH. [3]	+	+	+	+	+	+
Stenus lindbergi RENK.	—	—	—	—	—	—
Tetratoma fungorum FBR.	+	+	+	—	+	+
Trogophloeus nitidus BAUDI	—	—	+	—	—	—

[1] Wings of *Chrysomela haemoptera* are comparatively less developed than those of *C. hyperici* (see p. 245): particularly the apex is shorter. According to Rüschkamp (1927, p. 29) they are occasionally rudimentary, and I believe he is right in considering the species flightless.

[2] *Galeruca laticollis* has reflexed wings with strong veins. But they are not broader than the elytra, and the apex is rudimentary (cf. *G. oelandica*, p. 304).

[3] *Sitona humeralis* is dimorphic, according to Jackson (1928, p. 172). One individual from Åland and 2 from Skå were found to be macropterous. Later Palmén (in lit.) found one individual (macropterous) in drift material near Nl Tvärminne.

female). Thus direct dispersal in this way to Åland from Ösel-Dagö or Gotland cannot be ruled out. The nature of the currents in the Baltic Sea in autumn is highly favorable for such transport (Fig. 19b).

Eonius may also be suitable for hydrochorous transport. It is a stenotopic quicksand species found inland (Krogerus, 1932, p. 248) only as an Ancylus relict, otherwise living exclusively at the seashore, and therefore regularly getting into the sea at high tide. The insect must have arrived on the outer islands in the Gulf of Finland (Hogland, Lavansaari, Seiskari), possibly also in Fårön, by hydrochorous means.

244 **Table 16. Coleoptera (excluding Carabidae) of Al province (Åland), not found in east-central Sweden (Upl, Sdm, Vst, Nke)**

*—Absent throughout Sweden; P—Represented in drift material reported by Palmén (1944); b—Brachypterous; d—Dimorphic

		Acmaeops septentrionis Th.	P	*Chrysomela hyperici* Forst.[1]
	*	*Airaphilus perangustus* Har. Lindb.	P	*Coclambus marklini* Gyll.
	*	*Aleochara lygaea* Kr.		*Colon viennense* Hbst.
		Anthicus umbrinus Laf.		*Corticaria lambiana* Sharp
		Aphodius piceus Gyll.		*Cryptocephalus aurcolus* Suffr.
		A. plagiatus L.	*	*C. coerulescens* Sahlb.
	P	*Apion hookeri* Kirby	P	*Cryptophagus corticinus* Th.
		A. pisi Fbr.		*C. instabilis* Bruce.
		Atheta aquatica Th.		*Diphyllus lunatus* Fbr.
	P	*A. castanoptera* Mnh.		*Dorytomus salicis* Walt.
	*	*A. dubiosa* G. Bck.	b(♀)	*Drilus concolor* Ahr.
		A. dvinensis Popp.		*Dryops similaris* Boll.
245		*A. fungicola* Th.	b	*Eonius bimaculatus* Ill.
	*	*A. livida* Muls. rey.		*Ernobius pini* Sturm.
		Atomaria bicolor Er.		*Gnathoncus punctator* Rtt.
		A. södermani Sjöb.		*Haemonia pubipennis* Reut.
	*	*Attagenus schaefferi* Hbst.		*Heterhelus scutellaris* Heer.
		Bagous limosus Gyll.		*Heterocerus flexuosus* Steph.
		Berosus spinosus Stev.		*H. intermedius* Kies.
		Bidessus hamulatus Gyll.		*H. obsoletus* Curt.
		Bledius diota Schiö.	*	*Hololepta plana* Sulz.
	*	*B. rastellus* Schiö.	P	*Hylastes attenuatus* Er.
		B. tibialis Heer.	*	*H. brunneus* Er.
		B. tricornis Hbst.	P	*Hylobius transversovittatus* Gze.
	*	*Brachygluta helferi* Schm. Goeb.		*Laccobius decorus* Gyll.
		Bryoporus crassicornis Mäkl.		*Limnobaris reitteri* Munst.
		Calodera protensa Mnh.		*Liodes badia* Sturm.
	*	*Cassida stigmatica* Suffr.	*	*L. flavescens* Schm.
		Ceuthorrhynchus schönherri Bris.		*Mecinus collaris* Germ.
		Chromoderus fasciatus Müll.		*Meligethes morosus* Er.

Monochamus galloprovincialis Ol.
(d) *Mycetoporus aequalis* Th.[2]
P *Nanophyes circumscriptus* Aubé.
Noterus clavicornis Deg.
P *Ochthebius marinus* Payk.
Oxypoda brachyptera Steph.
Oxytelus sculpturatus Gr.
* *Pachyta quadrimaculata* L.
Philonthus addendus Sharp.
P *Phytobius velaris* Gyll.
P *Psylliodes isatidis* Heik.
Rhantus notaticollis Aubé
Rhynchaenus fagi L.
*b *Scleropterus serratus* Germ.[3]
* *Scymnus testaceus* Motsch.
Sitona cylindricollis Fåhr.[4]
* *Stenus lindbergi* Renk.
S. scabriculus J. Sahlb.
Tachyporus tersus Er.
Triarthron maerkeli Schm.
Trichomicra sahlbergiana Bernh.
Trogophloeus foveolatus Sahlb.
T. nitidus Baudi.

[1] In one specimen of *Chrysomela hyperici* examined from Skå the wings, well developed and with strong veins, are 1.5 times as long as the elytra. Rüschkamp (1927, p. 26), who had not examined *C. hyperici*, curiously believes that all species of *Chrysomela* being flightless genus is represented by 5 species, including *C. hyperici*, in drift material reported by Palmén (1944).

[2] *Mycetoporus aequalis* is dimorphic (Hellén, 1925, pp. 33, 40; Strand, 1946, p. 177); one individual from Al turned out to be macropterous.

[3] Palmén studied 17 Finnish specimens of *Scleropterus* for me, 15 from Åland. In all, the hind wings were totally reduced.

[4] According to Jackson (1928) *Sitona cylindricollis* is always macropterous.

Eonius is, ecologically and possibly dynamically, a perfect counterpart of *Cymindis macularis* among the carabids; they are the *only Coleoptera of Åland of which it must be assumed that they arrived only by the hydrochorous mode from the east* (*or southeast*). It is significant that both are found in Åland only on Eckerö, in the extreme west (for *Eonius*, see Håk. Lindberg, 1931, p. 153).

To assess the capacity of *Cymindis macularis* to tolerate hydrochorous transport, at least to get an idea, I carried out simple experiments on exposure to water (Experiments 143–145, p. 109) with 6 individuals each of this species and simultaneously of *C. angularis* and *C. humeralis*. Two serial experiments were attempted each with 3 × 3 specimens. In one the insects were left swimming undisturbed on the surface of the water, in the other the container was regularly shaken. The room temperature was high (20–25°C). The following results were obtained with *exposure to water*.

A. Undisturbed insects

No. of surviving specimens after	67 h	71 h	115 h	123 h	147 h	157 h	195 h	243 h	315 h	326 h
Cymindis angularis	3	3	3	2	2	2	2	2	1	—
C. humeralis	3	3	3	3	3	2	1	1	—	—
C. macularis	3	2	2	2	2	1	1	—	—	—

B. Insects in shaken containers

No. of surviving specimens after	13 h	28 h	43 h	52 h	60 h
Cymindis angularis	2	1	1	1	—
C. humeralis	2	1	1	—	—
C. macularis	3	2	—	—	—

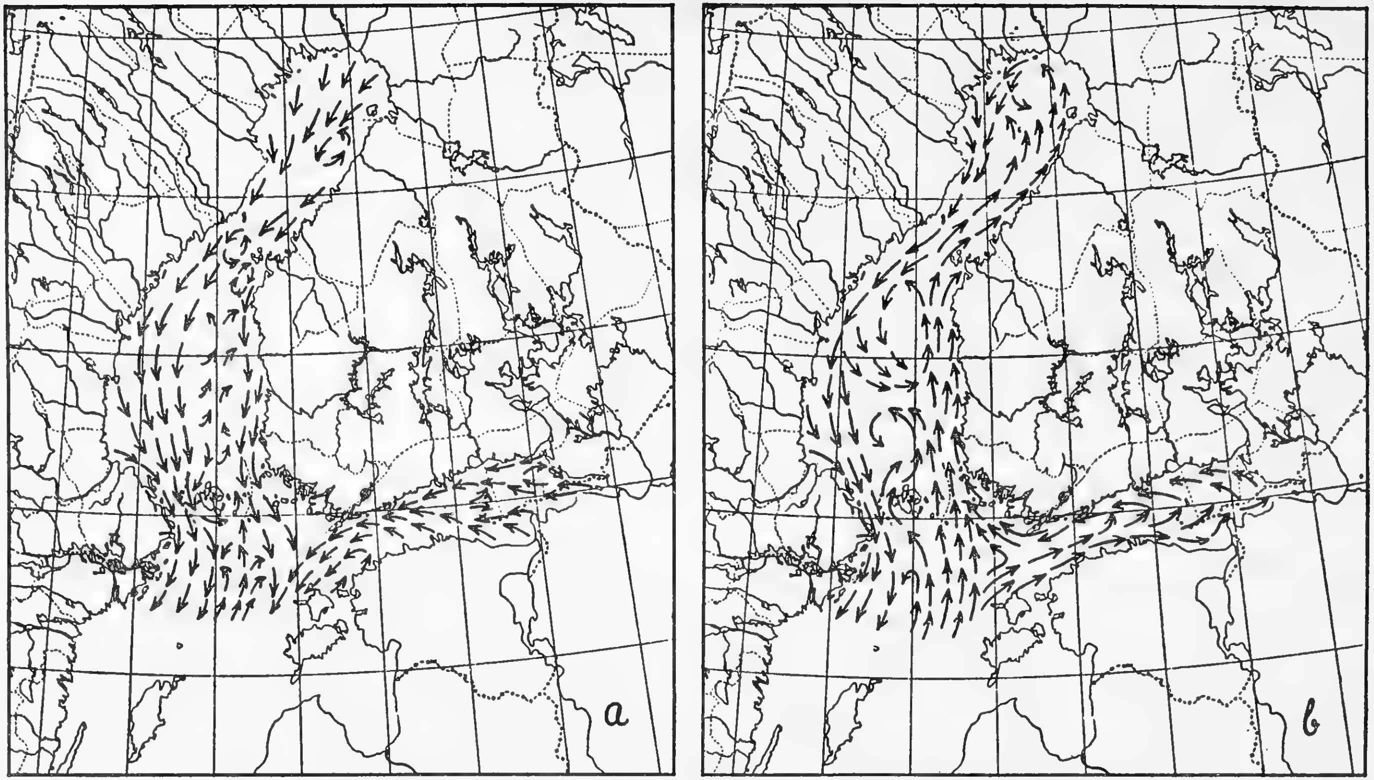
249 These experiments show (even taking into consideration the abnormally high temperature) that *Cymindis macularis* has little resistance to water, especially if splashed, and even less resistance than the 2 related species whose distribution provides no ground for presuming that they are dispersed by the hydrochorous mode. It is probable that *C. macularis* can tolerate long-distance hydrochorous transport (cf. p. 600) only with the help of floating objects like fascicles of *Elymus* and *Psamma*.

The situation is quite different for *Lycoperdina succincta*, *Chrysomela haemoptera* and *Galeruca laticollis*. None of these is a seashore species; the first two are xerophilous animals living in open, gravelly or sandy terrain; *Lycoperdina* is associated with puffballs, *Chrysomela* with species of *Plantago* (West, 1940–41, p. 494); *Galeruca* lives on green meadow soil, among others on *Thalictrum flavum* (West, l.c., p. 506). All three are to be considered as species with extremely poor dynamics. They naturally come next to the 6 flightless carabids discussed above (p. 241). —*Sclerопterus*, which has quite rudimentary wings, is enigmatic. In Fennoscandia it is found only in southwestern Finland (Ab, Nl) and in Åland. Its biology (host plants) and the modes of dispersal are unknown.

The coleopteran fauna of Åland on the one hand consists of an eastern (Finnish-Baltic) element, which with few exceptions is capable of flight and has certainly immigrated by the anemochorous mode (including anemohydrochorous), and on the other hand of a western (Swedish) element, of which at least 9 species must have immigrated by other modes (hydrochorous, zoochorous, or anthropochorous).

Evidently now an important task is to examine the validity of the rule that mainly aerial immigration has taken place from the east, so that it can be applied to other organisms. It is most natural to study the *phanerogamous flora*.

From a survey of the contributions by A. Palmgren (particularly 1927 and 1943–44) and Eklund (1927a, b; 1931) it might be possible to draw up lists of the "western" (Swedish) and of the "eastern" (Finnish-Baltic) species of the flora of Åland. Even though the allocation of many of these species in the
250 group concerned was based on more or less strongly motivated conjectures on the part of these authors, we may be justified in considering each group as a whole as fairly representative. The most important mode of dispersal of each species was then assessed, partly from the works of Eklund, Sernander



247 Fig. 19. Surface sea currents in the Northern Baltic Sea Basin:
a—in June; b—in October. Adapted from *Atlas öfver Finland* 1910 (Simplified).

(1901), Heinze (1932–35), Lagerberg (1937–39), and Romell (1938), and partly according to my own judgment. For nomenclature, *Stockholmstraktens Växter* (1937) is followed.

253 A survey of the plants listed above (Tables 17, 18) reveals the following:

The 129 "western" species in Åland include 27 anemochorous species, i.e. 21%.

The 63 "eastern" species in Åland include 9 anemochorous species, i.e. 14%.

The importance of anemochorous immigration to Åland is also evident for other plant species. Gustaf Haglund told me that all the *Taraxacum* species occurring in Åland are found in central Sweden. But *T. rubicundum* Dahlst., for instance also found there, is in no way synanthropic, and is unknown elsewhere in Finland and the entire eastern Baltics. —According to a communication by Herman Persson, among the *mosses* occurring in Åland, *Ulota drummondi* and *Douinia ovata* are unknown elsewhere in Finland and in the eastern Baltics but are found along the east coast of Sweden.

250–251 **Table 17. Phanerogamous plants ("large species") of Åland province that can be considered (at least partly) as immigrants from Sweden**

*—Dispersal (mainly) anemochorous

	Adoxa moschatellina		C. extensa
	Agrimonia odorata		C. hirta
	Aira praecox		C. lepidocarpa
	Androsace septentrionalis		C. livida
	Anthyllis vulneraria		C. loliacea
	Aquilegia vulgaris		C. montana
	Arctium nemorosum		C. nemorosa
	Asperula odorata		C. ornithopoda
	A. tinctoria		C. paradoxa
	Athamanta libanotis		C. polygama
	Barbaraea stricta		C. remota
	Brachypodium silvaticum		C. riparia
	Bromus benekenii		C. vaginata
*	Calamagrostis arundinacea		C. vulpina
	Calamintha acinos		Ceratophyllum demersum
	Callitriche autumnalis	*	Chimaphila umbellata
*	Campanula latifolia		Cochlearia danica
	Cardamine flexuosa	*	Coeloglossum viride
	Carex aquatilis		Corydalis intermedia
	C. arenaria		C. laxa
	C. caespitosa	*	Crepis paludosa
	C. caryophyllea	*	C. praemorsa
	C. digitata	*	Cypripedium calceolus

* Epipactis latifolia
* E. palustris
251 * Eriophorum gracile
* E. latifolium
Erysimum hieraciifolium
Fragaria viridis
Fritillaria meleagris
Gagea lutea
G. minima
Galium trifidum
Gentiana campestris
G. uliginosa
Geranium columbinum
G. dissectum
G. lucidum
Glechoma hederacea
* Herminium monorchis
Hippophaë rhamnoides
Hydrocharis morsus-ranae
* Hypochaeris maculata
Jasione montana
* Lactuca muralis
* Lathraea squamaria
Lemna trisulca
Litorella uniflora
* Malaxis paludosa
Medicago lupulina
Melica uniflora
Mentha litoralis
Mercurialis perennis
* Microstylis monophylla
* Monotropa hypopitys
Myriophyllum verticillatum
Myosotis palustris
Najas marina
* Neottia nidus-avis
Nuphar luteum
N. pumilum
Odontites litoralis
Oenanthe fistulosa
* Ophrys muscifera
* Orchis incarnata (coll.)
* O. sambucina
* Orchis traunsteineri
Phloeum boehmeri
Polygonum viviparum
Potamogeton crispus
P. polygonifolius
P. praelongus
Potentilla tabernaemontani
Ranunculus circinatus
R. lingua
Rhynchospora alba
Rosa tomentosa
Rubus pruinosus
Rumex hydrolapathum
Sagina maritima
* Salix livida
Salsola kali
Samolus valerandi
* Saxifraga granulata
Scheuchzeria palustris
Scirpus maritimus
S. rufus
Sedum annuum
S. rupestre
S. sexangulare
Selinum carvifolia
* Solidago virgaurea
Sorbus fennica
S. suecica
Sparganium affine
S. ramosum microcarpum
Spergula vernalis
Stellaria nemorum
Taxus baccata
Torilis anthriscus
* Ulmus glabra
Veronica anagallis-aquatica
V. beccabungae
Vicia lathyroides
Viola rupestris
V. stagnina

254 It may be concluded that *the indication obtained from Coleoptera, that anemochorous dispersal has taken place to Åland mainly from east to west, is not confirmed by a study of plants.*

252 **Table 18. Phanerogamous plants ("large species") of Åland province that can be considered (at least partly) as immigrants from Finland or Baltics**

*—Dispersal (mainly) anemochorous

*	Acer platanoides
	Agrimonia eupatoria
	Ajuga pyramidalis
	Alliaria officinalis
	Allium ursinum
	Alopecurus ventricosus
	Arbis hirsuta
	Arrhenatherum elatius
	Artemisia campestris
	Atriplex hastata
	Avena pratensis
	Brachypodium pinnatum
	Cakile maritima
	Calystegia sepium
	Cardamine hirsuta
	Carex brunnescens
	C. distans
	C. glareosa
*	Cephalanthera longifolia
*	Cirsium heterophyllum
	Clinopodium vulgare
	Crambe maritima
	Crataegus curvisepala
	C. monogyna
	Daphne mezereum
	Draba incana
	Geranium pratense
	G. sanguineum
*	Gymnadenia conopea
	Honckenya peploides
	Hypericum hirsutum
	Isatis tinctoria
	Juncus balticus
	Knautia arvensis
	Lepidium latifolium
	Melampyrum cristatum
	Melandrium viscosum
	Myosotis collina
*	Orchis mascula
	Origanum vulgare
	Polygala amarella
	Polygonatum multiflorum
	Polygonum dumetorum
*	Picea excelsa
	Plantago lanceolata
	Ranunculus cassubicus
	R. ficaria
	Rhamnus catharctica
	Salicornia europaea
*	Salix rosmarinifolia
*	Saxifraga tridactylites
	Scleranthus annuus
	Scutellaria hastifolia
	Silene venosa
	Stachys silvatica
	Stellaria holostea
	Suaeda maritima
	Succisa pratensis
	Thymus serpyllum
*	Tilia cordata
	Trifolium montanum
	Veronica spicata
	Viola uliginosa

Actually the documented evidence of a *western* anemochorous element in the case of plants, apart from the short distance across the sea, also seems to be supported by the wind conditions prevailing around Åland (Fig. 20). Easterly or southeasterly winds do not prevail at any time of the year. The dominance of southwesterly winds in autumn, the most important period for dispersal of most of the species, is striking. Even in the higher atmosphere in these areas, especially during the summer half-year, westerly winds prevail (Östmann, 1933, p. 30).

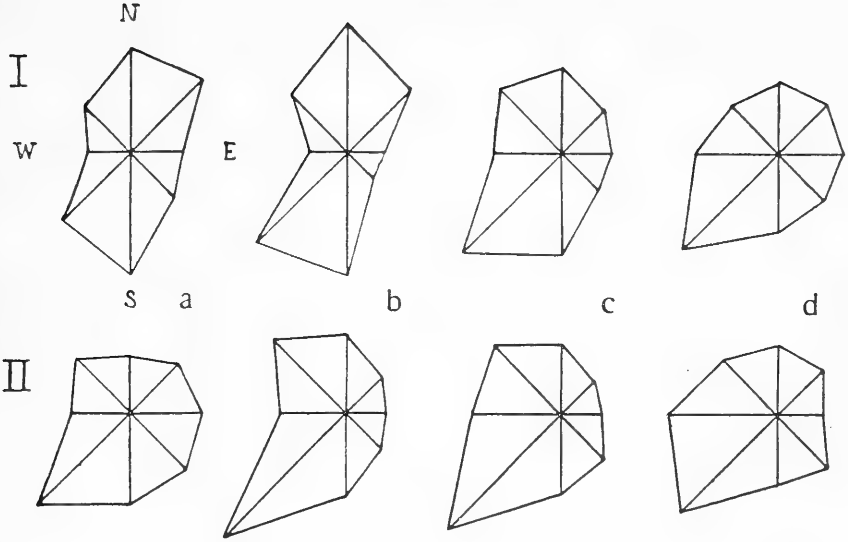


Fig. 20. Wind roses† in Åland (1886–1905). I—Sälskär (N of Åland); II—Bogskär (S of Åland). a—Spring; b—summer; c—Autumn; d—Winter.

From *atlas öfver Finland*, 1910.

On the other hand I do not believe that the major component of an eastern anemochorous element in the beetle fauna can be explained simply by the fact that the animals fly mainly in spring—which actually happens in the case of carabids (see p. 580)—for even at that time of year southerly and southwesterly winds are commoner than easterly or southeasterly ones. —The habit of carabids of flying (p. 584) against the wind may be ignored as well, since they are such weak fliers that they are carried away even by very light winds (> 2m/sec).

However, the physiological difference between animals and plants is very important. The diaspores of plants can drift for weeks and months in the Baltic Sea water without losing their capacity to germinate (Eklund, 1927a, b; 1929). This amply explains the substantial admixture of those plants in the flora of Åland, which have dispersed hydrochorously from the eastern Baltics (Eklund, 1931). On the other hand, in the drift material of insects along the southern coast of Finland no species was found that must have crossed the Gulf of Finland by purely hydrochorous means (Palmén, 1944). Such cases may occur (p. 603), but only as rare exceptions.

†("Windrosen" = wind directions; suppl. scient. edit.)

Two problems have here to be dealt with more specifically:

1. In the colonization of Åland, why has anemochorous immigration coming from the east played a greater role in the case of beetles than in the case of plants?

2. How have the flightless "Swedish" beetles reached Åland?

255 1. The first question may concern not only Åland but the Baltic Sea region in general. Later we will deal with the considerable eastern element in the fauna of Gotland and neighboring islands, which has arrived by the anemochorous mode. Then it is also appropriate to point out the oddity that 4–5 carabid species have reached Sweden from Finland by crossing Kvarken (the
256 narrowest part of the Gulf of Bothnia) through the air (p. 593), whereas there is no evidence to show that immigration of any species has taken place from the opposite direction.

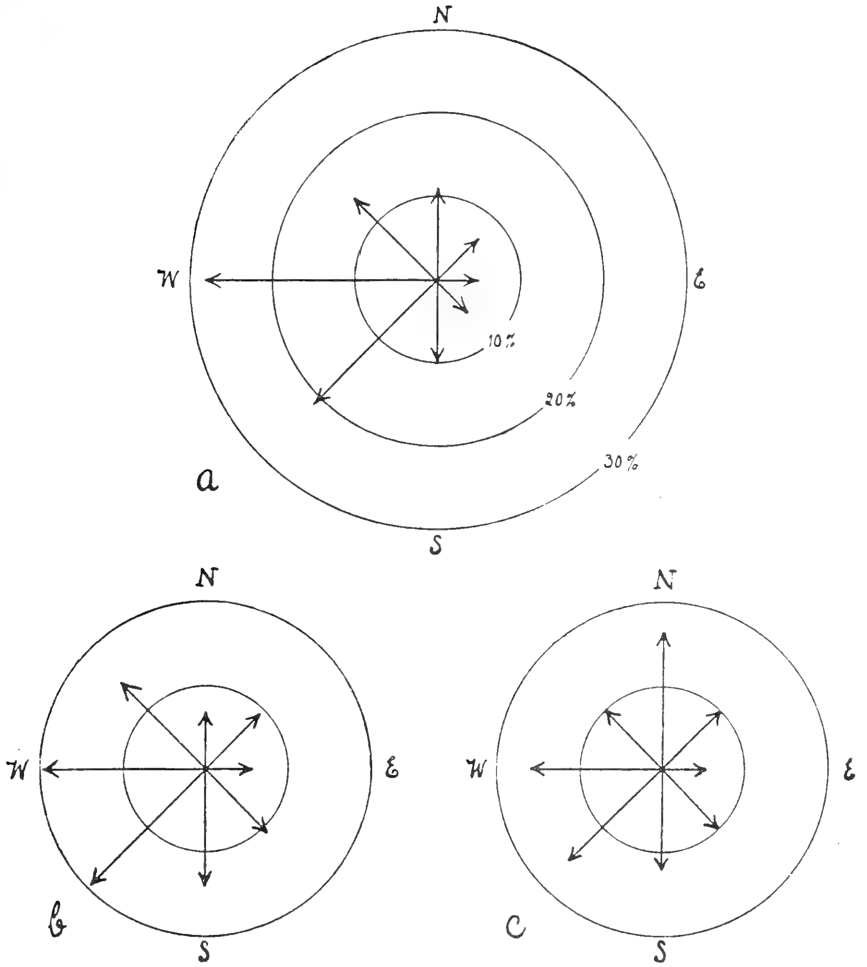
Thinking about this, it occurred to me that: many beetles capable of flight, including some carabids, fly in the evening or afternoon when the air has warmed up. Could it be that these animals, especially those flying in the afternoon, fly *toward the sun*, or at least show a preference for this direction? Then the dispersal of the species would be mainly *toward the west*.

It appeared possible to study this problem experimentally. For this purpose I devised a "flight direction apparatus" (Fig. 8, p. 109), in which certain species that are comparatively active fliers were studied (Experiment 147 ff., p. 110). The experiments were all carried out between 5 p.m. and 7 p.m. and one of the eight sectors of the apparatus was directed exactly toward the sun (west). Only in the case of 3 species (*Oodes gracilis*, *Acupalpus consputus*, *A. dorsalis*) was the observation material large enough (> 90 cases) for the "flight roses" to be drawn (Fig. 21).

The result of these experiments is so unambiguous that there is no room for experimental error or coincidence. A strong inclination to fly *toward* the sun is shown in particular by *Oodes*. That this is not so consistently evident in both the species of *Acupalpus* may be due to the fact that they take off in the air more or less spirally, in contrast with *Oodes*, which usually takes off in the final direction of flight. I believe that by using a larger apparatus the species of *Acupalpus* would also show "better" results.

It is advisable to express the results numerically in such a way that the animals that entered the three "western sectors" are compared with those of the three "eastern sectors." In this way species of *Badister* are also taken into consideration, although the material available was insufficient (Table 19).

We find that in the species observed, with the exception of *Badister peltatus* (for which too little material was available), the inclination to fly toward the sun is very pronounced. Being more or less typical evening fliers, they must therefore *disperse more toward the west than toward the east*, provided there are no strong winds in the opposite direction. This seems to be an important factor which has influenced the considerable immigration of flying Coleoptera



255 Fig. 21. "Flight roses". Percentage distribution of individuals observed in the flight direction apparatus (Fig. 8, p. 109), between 5 p.m. and 7 p.m. in bright sunshine. a—*Oodes gracilis* (100 specimens); b—*Acupalpus consputus* (200 specimens); c—*A. dorsalis* (91 specimens). Experiment 147ff., p. 110.

to Åland from the east and has also influenced the fauna of the other Baltic
257 islands (see below). The general consequences of this observed phenomenon will be reported in a later section (p. 592 ff.).

2. It remains to be considered why the transport of *flightless* species to Åland has been more from the west than from the east (p. 249). Two possible explanations may be given.

a. The species in question could have arrived anthropochorously, predominantly from Sweden, since in earlier times Åland had active trade connections with that country.

b. The dispersal could have taken place mainly *hydrochorously*, and the shortest water crossing west of Åland would have facilitated transport from Sweden.

Theoretically speaking, zoochorous dispersal (supposedly only by birds) is also conceivable. But as discussed elsewhere (p. 605), hardly any significance should be attached to this mode of dispersal, particularly with respect to carabids, so that it can be ignored here.

a. The *anthropochorous* dispersal of carabids is also discussed elsewhere (p. 606) in detail, where I suggest that it has generally been overestimated. In the case of Åland in particular, the following facts may be stated: The only two functionally brachypterous species occurring in Åland that can be certainly designated as synanthropous, namely, *Bembidion ustulatum* and *Carabus nemoralis*, are both extremely rare in Åland. Altogether 3 specimens of the
258 former species have been found at 3 different localities, and *Carabus* has been found only once in Eckerö in the west. All these observations are recent, at any rate after 1930. The climatic conditions do not provide any explanation for this sparse occurrence in Åland, since the species in question extend much farther north on the mainland on both sides of the Bothnian Sea. The two remaining brachypterous carabids of the Stockholm region (and of the entire "region of comparison" 2a) which are markedly synanthropous, namely, *Pristonychus terricola* and *Stomis pumicatus**, have not reached the mainland of Åland, but the former was found in 1944 in Ab Korpo, an island that has trade connections chiefly with Åbo, where the species has long been recorded.

It is thus striking that the immigration of synanthropous species to Åland

Table 19. Distribution of 6 carabid species in the flight direction apparatus. Experiments 147–152 (p. 110)

	Number of observed cases	Western sectors		Eastern sectors		Ratio
		Number	%	Number	%	West : East
Oodes gracilis	100	63	63	17	17	3.7
Acupalpus consputus	200	107	53.5	51	25.5	2.1
A. dorsalis	91	39	43	23	25	1.7
Badister dilatatus	34	19	56	7	21	2.7
B. unipustulatus	27	16	59	3	11	5.3
B. peltatus	15	3	20	11	73	0.3

**Stomis* is markedly synanthropous only in the northern part of its area.

that are flightless and thus dependent chiefly on anthropochorous dispersal has taken place in an extremely fortuitous and ineffective manner. It is all the more improbable to explain the presence of the entire functionally brachypterous element in the fauna of Åland by such transport (chiefly from Sweden). The completely normal composition of the element is evident from the fact that of the constantly brachypterous non-synanthropous carabids of the Swedish area of comparison in Upl (2a, map in Fig. 18), only the following 4 species are missing from the mainland of Åland: *Agonum ericeti, Carabus coriaceus, C. glabratus, C. problematicus.*

b. We therefore have to *assume immigration by a predominantly hydrochorous mode of transport, chiefly from Sweden** for the functionally brachypterous carabids of Åland.

This applies chiefly to the following 6 species of carabids and 3 species of chrysomelids:

Calathus fuscipes	*Olisthopus rotundatus*
Dromius linearis	*Chrysomela haemoptera*
D. nigriventris	*Galeruca laticollis*
Licinus depressus	*Lycoperdina succincta*
Metabletus foveatus	

Keeping this possibility in view, when we study the surface currents of the surrounding sea (Fig. 19) we nevertheless find that in the strait which sepa-
259 rates Åland from Sweden (Upl) they follow a highly unfavorable course. Along the Swedish (Uppländish) coast the direction of the current throughout the year is markedly southward. In spring this is true for the entire strait reaching up to Åland. Only in autumn does a northward current also appear immediately off the west coast of Åland. Animals which happen to get in distress at sea along the part of the coast of Uppland that lies nearest to Åland must inevitably be carried south, and they must have already passed the latitude of Åland before they are able to cross over, even when they are gradually pushed eastward by waves caused by a strong westerly or southwesterly wind. Transportation to Åland is possible, at least theoretically, only if the starting point of the hydrochorous transport is placed farther north (at least up to northern Upl). However, the Swedish northern limit is situated farther *south* than Åland for no fewer than 5 of the 9 species susceptible of such transport, i.e., *Dromius linearis*, *Licinus depressus*, *Chrysomela haemoptera*, *Galeruca laticollis*, *Lycoperdina succincta*. The objection that these limits were possibly situated farther north during the postglacial warm period is irrelevant in the present context, since colonization of Åland was impossible during most of this period. Even during the Old Stone Age, Eckerö comprised at the most two bare rocky skerries above the sea level at that time (Hausen, 1910a, map).

*For the possibility of anemochorous transport, of flightless insects too, see p. 590.

There is, however, an exceptional case of hydrochorous transport, where the currents play a smaller role, and the winds have a correspondingly larger role: *the drifting of ice in early spring* (for its occurrence in the sea W of Åland, see maps by Erik Palmén in Hausén, 1946, pp. 107–108). Given sustained westerly to southwesterly winds (see wind roses, Fig. 20), ice-floes emanating from the coast of Uppland, crossing the relatively weak currents (Hausen, l.c., p. 97), can be carried to western Åland. The ice-floes may include ones that were earlier squeezed together and pushed onto the beaches of the Swedish coast by easterly winds, where they might easily be covered with reeds, litter, etc. Such ice-floes, strewn with remains of plants, are frequently observed during spring passages in the Skärgård of Stockholm. It may also be noted that at this time the hibernating insects are still more or less stiff and motionless, with low respiration, so they can better endure the adversity of a passage in spite of being drenched from time to time, and make
260 no attempt to escape. Shore beetles can even endure freezing in solid ice for months, if reeds or other hiding places are present (Palmén, 1945a; see also p. 600).

A detailed argument was provided above (p. 205) as to why passive transport of insects is more likely to lead to permanent colonization if it takes place in the adult stage. If the preceding exposition is correct, according to which the flightless carabids reached Åland from Sweden chiefly by ice transport, it must be expected *that those flightless species that hibernate as adults are favored for the colonization of Åland.* Table 13 (p. 230; last column) actually shows *that out of all the islands of the Baltic Sea area considered, Åland shows the fewest larval hibernators.* This is strong evidence for the above hypothesis.

In conclusion the following statement may be made on the immigration of the beetle fauna of Åland:

The small number of flightless forms is characteristic for the Fasta-Åland fauna, especially as compared with that of the Skärgård situated east of it. This element has colonized Åland chiefly from Sweden, and by means of hydrochorous transport. The main immigration route of the flying species, however, is from the east and southeast (Finland and eastern Baltics). Some of this immigration has also reached the central Swedish mainland (p. 719).

3. The southwest-Finnish Skärgård

In the tables this region is indicated as the "Skärgård of Åland." This is strictly incorrect, because most of the islands are located in the Province of Ab, eastward as far as Nagu. It is a very scattered archipelago, consisting of tens of thousands of islands and bare rocky skerries, situated at a much lower level than the main island of Åland. Even the larger islands are almost all only 20–30 m above sea level (Hausen, 1910b, pp. 2, 6). Only some points reach a few meters (< 50 m above sea level) higher (Bergroth, 1894, p. 8; Eklund,

1931, p. 11; Hausen, 1946, p. 17). Hence the entire area of rocky skerries is very young, and the first bare rocks emerged from the sea only at the beginning of the Littorina period.

The population is fairly dense and the larger islands are more or less cultivated. The trade connections, especially with Åbo, are active.

261 The rich flora, which is largely similar to that of Fasta-Åland, is dealt with in the works cited above (p. 249).

With regard to Coleoptera, only a few of the larger islands or island groups have been explored more thoroughly, primarily Föglö, Kökar, and Korpo, and in addition Sottunga, Kumlinge, Houtskär and Nagu. The composition of the carabid fauna naturally also shows a close relationship with Fasta-Åland. It is of course poorer, with only 124 species (as against 157), which include the following 10 species not found on Åland:

Agnoum moestum	*Dromius quadrinotatus*
Amara crenata	*Harpalus luteicornis*
Bembidion grapei	*H. punctatulus*
Carabus convexus	*Panagaeus bipustulatus*
Cymindis vaporariorum	*Pristonychus terricola*

Of these, *Agonum, Amara* and *Panagaeus* are to be considered easily as accidental immigrants from the south, and perhaps also *Bembidion grapei* and *Harpalus punctatulus*, although at least the former may have originated from the Finnish mainland. *Pristonychus* is synanthropous and anthropochorous. The two functionally brachypterous species, *Carabus convexus* and *Cymindis vaporariorum*, are of special interest.

On the whole, *the brachypterous element* of this Skärgård region deserves special attention. Compared with the "region of comparison," it is *larger than that of any of the Baltic Sea islands here considered* (Table 12). This is not to be understood as having immigrants of anthropochorous transport (cf. Åland above). The reason must be that the Skärgård region in question, due to its special features, is suitable for hydrochorous colonization. This is all the more striking in view of the young age of these islands, which is evident from a comparison with the outer islands of the same age in the Gulf of Finland, and with Gotska Sandön (see below).

The usual freezing of the entire Skärgård sea (Fig. 22) seems to be especially favorable for transport by ice in early spring. However, if this represents the most important mode of colonization, one would expect a deficit of larval hibernators, as in the case of the mainland of Åland. But this is not the case (Table 13). It is therefore not rash *to assume, in addition, a strictly hydrochorous transport during the summer half-year from the Finnish mainland.* The surface currents of the sea are especially in favor of it in autumn (Fig. 19, p. 247).

262 The tens of thousands of islands and rocky skerries of the Skärgård region of southwestern Finland have functioned as a fine-mesh sieve, representing a big obstacle for the dispersal of hydrochorously transported insects from Finland to Fasta-Åland. This is hardly less true for anemochorously dispersed animals. Let us visualize concretely what happens if a living, hydrochorously transported *flightless* animal or an anemochorously carried animal capable of *flight* lands on an islet of the Skärgård in vital condition. If favorable conditions for survival exist both kinds will stay and, under the most propitious circumstances (impregnated females or several individuals arriving simultaneously), may realize a permanent colony. But in the vast majority of islands, at any rate on small rocky skerries the requirements for life for these species are lacking. What happens then? The winged animal flies on after forlorn search, toward an uncertain (but possibly lucky) fate. But the flightless animal stays
263 on. It does not voluntarily jump into the sea in order to swim to new areas. Only an accident can take it there, just as originally it was an accident that it came into the water. On the contrary, the winged animal at one time, at the original starting point, *voluntarily* opened its wings, and can always repeat this action in *voluntary flight*. For such an animal the thousands of islands are welcome places of rest, at least after an anemohydrochorous adventure, and before starting for new trips. We may thus conclude that *a dense, widely scattered Skärgård offers an excellent springboard for the flying forms for further dispersal*; *for the flightless forms it functions as an obstacle*, *as compared to the open* (*but moderately wide*) *sea. This provides an important additional clarification of the fact that Fasta-Åland has obtained flying forms chiefly from the east and flightless forms largely from the west.* However, these points are evidently not applicable to plants.

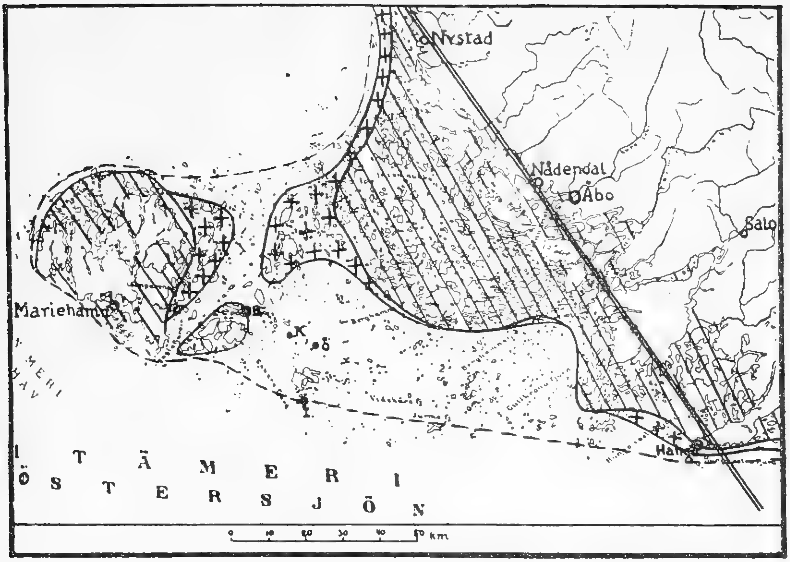
However, it cannot be denied that, especially for the colonization of the smaller outer rocky skerries, anthropochorous transport in hay-boats has played an important role, also with respect to insects, as has been vividly illustrated by Eklund (1931, p. 69). Such a role is nevertheless quite modest in my opinion.

4. Hogland

Hogland differs from the remaining so-called outer islands of the Gulf of Finland in several significant ways. Primarily it is much older, older even than Åland.

The highest point is 158 m above sea level, which shows that Hogland was never submerged completely during the postglacial period (Sauramo, 1942, maps on pp. 227–228). The distance from the Finnish mainland is 43 km, that from the nearest wooded islets about 20 km; Estonia lies 55 km away.

Hogland actually represents a continuous basement complex rock formation. It is 11 km long and up to 3 km broad and almost everywhere rises steeply from the sea. The region is about 20 km^2, one-half of which is covered with



262 Fig. 22. Maximum extent of solid ice in the Skärgård of southwestern Finland in mild winter (hatched and crossed ["blue ice"]) compared with normal winter (broken line). After Nordman (1943).

forest (chiefly *Abies* and *Pinus*) (Välikangas, 1936, p. 513). In the lowlands along the coast there is also an admixture of deciduous trees, but there is no purely deciduous forest (Nordling, 1904, p. 122).

264 In the interior there are a few small lakes (altogether covering about 19 ha); there are no swamps or bogs. The seashore is uniformly rocky or stony; only at one place is there a short sandy strip.

The population of the two villages is about 900 people. They originally came from Virolahti (Vederlaks) on the Finnish mainland (Province of Ka) (Ramsay, 1896, p. 57), and there have always been stronger connections with Finland than with Estonia. There is not much cultivation.

Hogland is to be considered a region strikingly poor in biotopes, and the flora is correspondingly poor (M. Brenner, 1871; Saelan, 1900). However, the carabid fauna, with 87 species, is unexpectedly rich, especially in comparison with the remaining outer islands, and some species possibly remain to be discovered. The xerophilous element is more poorly represented than on any of the other Baltic Sea islands (Table 14). Instead there is a preponderance of forest species. With respect to dynamics, as on almost all the islands, the fauna shows a predominance of dimorphic species (Table 10). But so far as is known, in seven out of 18 cases these occur only in the macropterous form

(Table 11), so that there is a distinct deficit of the functionally brachypterous group (Table 12). It is much less than in the case of the remaining outer islands to be considered below.

For a more precise comparison it is advisable to place the functionally brachypterous (or dimorphic) species of all the outer islands side-by-side. The few records from Peninsaari Island were not considered, nor the dimorphic species *Carabus clathratus,* the condition of whose wings could not be determined (Table 20).

266 It is at once evident that of these 27 species only one, *Pterostichus diligens*, is common to all four islands. Among the 89 functionally macropterous carabids of the outer islands (cf. list on p. 270), on the other hand, the following 9 species (a good 10%) are common to all four islands:

Agonum marginatum
A. sexpunctatum
Bembidion obliquum
B. quadrimaculatum
B. rupestre
B. saxatile
Harpalus aeneus
H. pubescens
Pterostichus nigrita.

Of these only the two species of *Harpalus* are to some extent favored by cultivation, and may thus have been introduced anthropochorously.

The obvious conclusion is: The capacity to fly allows a *rapid* and apparently "consequent" colonization of habitable regions. But if *sufficient* time is available even the soil-bound, flightless faunal element reaches its destination, even though it may be unfavorably located (within reasonable limits). Hence of the above 27 flightless species of the outer islands only four are missing from Hogland, all of which are species of open terrain, and a fifth (*Bembidion lampros*) was found there only in macropterous form.

None of the 22 functionally brachypterous species of Hogland is associated with human culture (anthropobiont), and only 2 species (*Patrobus atrorufus* and *Pterostichus vulgaris*) are to some extent considered cultural beneficiaries (anthropophilous). Among species of the same ecological type apparently missing on Hogland, although widely distributed on both sides of the Gulf of Finland and more or less common, mention may be made of the following: *Amara apricaria*, *A. eurynota*, *A. ingenua*, *Bembidion ustulatum*, *Carabus cancellatus*, *C. nemoralis*, *Pterostichus coerulescens*. Of these the species of *Carabus* and *Bembidion* are functionally brachypterous. In my view these facts indicate *that anthropochorous dispersal had at the most a subordinate role in the colonization of Hogland.*

As in the case of Åland and the entire southwestern Skärgård, we should thus ascribe the richly represented flightless faunal element of Hogland chiefly to a hydrochorous transport. Since, in clear contrast to the insular regions mentioned, *it shows a considerable preponderance of larval hibernators*
267 (Table 13), it must be assumed *that this transport took place chiefly in summer.*

I am unable to decide whether this is due to unfavorable ice-drift conditions (cf. Tytarsaari, p. 272). It of course needs to be pointed out that the southern shore of the Gulf of Finland, where the main current of the surface water touching Hogland originates in spring (*Atlas öfver Finl.*, 1910, map 9), is ice-free earlier than Hogland (Ibid., map 6b). There is very small possibility of the ice from this coast landing at Hogland.

If we study the surface currents of the sea in the Gulf of Finland (Fig. 19, p. 247), which vary considerably in different years (Witting, 1911, p. 46), we find that especially in early summer they are not unfavorable to a fairly straight journey from deep in the gulf to Hogland. The turbulence occurring around this island might even bring about a concentration of transported materials. The map given by Palmén (1944, p. 66) shows the currents in late summer, when Hogland comes in contact chiefly with the eastward current, which signifies a longer transport route from the north coast of Estonia. I therefore find that Palmén's discussion (l.c., p. 81), according to which more or less direct hydrochorous transport across the Gulf of Finland (Estonia—southwestern Finland) is impossible, does not apply to the conditions prevailing in spring and early summer. It is indubitable that the flightless beetles have also colonized Finland by this route (p. 603).

It may not be possible to decide whether Hogland received its hydrochorously immigrant species from Finland or from Estonia. Its functionally brachypterous species are widely distributed in both countries, with the exception of *Bembidion schüppeli* and *Carabus problematicus*, which require further discussion.

The species of *Bembidion* occurs here in brachypterous form, whereas only the macropterous form was found in the drift material from the Tvärminne area (Nl). The south Finnish-Estonian subarea of the species has a markedly relict character, early postglacial stock, which established itself in the regions first colonized. The question arises whether Hogland was part of these regions.

Still more striking is the record of *Carabus problematicus,* which is otherwise known in Finland exclusively from Petsamo, and is missing from northern and western Russia. Its occurrence in the Baltics is based on dubious
268 records. The animal from Hogland was described as a different "morph" (Hellén, 1934, p. 41). But to this, much importance cannot be attached since it was based on a single specimen (Krogerus later found fragments of a second specimen). At any rate this undoubtedly represents a very old inhabitant of the island. In Scandinavia *C. problematicus* is certainly a Würm hibernator, even in the highest northern part. It is to be assumed that even in Finland it closely followed the melting ice edge as well. It must be borne in mind that at the time of the "Baltic Ice Sea," Hogland remained above water, whereas the entire southern coastland of Finland was covered with water up to the edge of the ice. A few islands occurred at the Isthmus of Karelia and NW of Ladoga (Sauramo, 1942, map on p. 227).

265 **Table 20. Functionally brachypterous (or dimorphic) species of the outer islands in the Gulf of Finland**

m—Macropterous form only; d—Both forms of dimorphic species

	Hogland	Tytärsaari	Lavansaari	Seiskari
Agonum fuliginosum	+	–	+	–
Bembidion lampros	(m)	–	+	(m)
B. schüppeli	+	–	–	–
B. unicolor	+	–	–	–
Calathus erratus	+d	+	–	+d
C. melanocephalus	+	(m)	–	–
C. micropterus	+	–	–	–
Carabus granulatus	+	–	+	+
C. hortensis	+	–	–	–
C. nitens	–	+	–	–
C. problematicus	+	–	–	–
Cychrus caraboides	+	–	–	–
Cymindis angularis	–	+	–	–
Dyschirius globosus	+	+	–	+
Leistus ferrugineus	+	–	–	–
L. rufescens	+	–	–	–
Metabletus truncatellus	+	–	–	–
Notiophilus aquaticus	–	–	+	–
N. palustris	+d	–	–	–
Patrobus atrorufus	+	–	–	–
Pterostichus diligens	+	+	+	+
P. lepidus	–	–	–	+
P. minor	+d	(m)	–	–
P. strenuus	+	+	–	–
P. vernalis	+d	+d	(m)	–
P. vulgaris	+	+d	+	–
Trechus secalis	+	–	–	–

Poa alpina and *Viscaria alpina* in the flora of Hogland (M. Brenner, 1871, p. 13) can be considered as counterparts of these beetles.

Miscodera arctica likewise represents a northern and certainly an early immigrant. It is numerous only in the fjelds, but has been recorded in southern Finland by a few specimens, in Estonia actually by only one specimen. —In its history of immigration, *Nebria gyllenhali* corresponds with the three species considered. However, since it is widely distributed along the north coast of Estonia a later immigration from there is conceivable. It of course also occurs on Åland. —Both species are capable of flight.

5. The Remaining Outer Islands

Only Tytärsaari, Lavansaari, and Seiskari are treated here because the other, smaller islands received only cursory study (Rosberg, Grotenfelt, Hilden, and Wecksell, 1923).

Tytärsaari, about 17 km SSE of Hogland, is the highest and consequently oldest of these islands. It is almost circular, 8.2 km^2 in surface. The highest point, about 50 m above sea level (Rosberg, 1898; Välikangas, 1936, p. 513) is in the north where, as in the west, it has mountainous terrain (basement complex). This may have already emerged from the sea at the end of the Yoldia period, existing only as bare rock for thousands of years (Sauramo, 1942, map on p. 231). The distance from Estonia is 43 km and from the Finnish mainland about 65 km. In the south and the east the island is quite sandy, in the east there is even quicksand along the seashore. There are also gravelly and stony shores and at one place a small moist shore-meadow. The only bodies of fresh water are small lagoons and a brook near the village. The island is largely wooded, chiefly with *Pinus*, in the south predominantly with *Abies* and here
269 and there an admixture of *Betula*, etc. (M. Brenner, 1871; Olsoni, 1927). —The population, more than 500, lives in one village in the south. The people came from Finland but the contacts have been mainly with Estonia, from where there was once considerable import of potatoes, hay, etc. Välikangas (1930, p. 76) believes that this explains the surprising occurrence of *Eliomys quercinus* on the island. Since there is no harbor, all freight must be transhipped in small rowboats. Cultivation is slight and consists chiefly of dry meadows and potato fields.

The native flora is not rich. The carabid fauna includes more species than those of the other two islands, which is primarily due to better exploration.

Lavansaari is situated 43 km E of Hogland and about 33 km from Tytärsaari. It is likewise nearly circular but has a more irregular shape; the former islet Suisaari has now merged with it. The region is almost 16 km^2. There is no outcropping mountainous terrain, but the entire island consists of sandy moraine, which at some places on the shore merges into quicksand. The highest point is about 20 m above sea level (Krogerus, 1932, p. 61). Thus, the island may have finally stabilized only after the maximum rise in sea level ("Transgression") of the Littorina period, about 4,700 years ago (Sauramo, 1942, p. 242). The distance from the coast of Ingermanland is 25 km and from the Finnish mainland a good 50 km. In the south there is a lake more than one km long, from which a rivulet runs into the sea. Furthermore, the island is poor in biotopes. Deciduous trees have a smaller role than in Tytärsaari. On the other hand, the littoral flora is richer (M. Brenner, 1871, p. 10). —The population, about 1,340 (1921), is restricted to three small villages in the northwest. Cultivation (gardens, potato fields) is very poor. In recent decades the trade connection has been chiefly with Kotka and Viborg, but earlier with Leningrad and Narva too.

The coleopteran fauna has not been fully explored.

Seiskari is situated 25 km E of Lavansaari, a good 20 km from the coast of Ingermanland and almost 40 km from the Finnish mainland (Ik). It is 4 km long and about 4 km^2 in surface. The highest point is about 15 m above sea level. Seiskari is thus *the youngest* of the three islands. The eastern part of the island is gravelly-stony, wooded (mostly *Pinus*), and the shores are mainly stony and slimy (Krogerus, 1932, p. 60). The western shore consists of highly mobile quicksand. There is no running fresh water, only a few bogs and ponds. The vegetation is generally scanty and the flora is poor in species.

270 The population, about 850 (in 1921), is restricted to three villages on the west coast. Cultivation is extremely poor. In earlier times there was active contact with Leningrad and Narva but now chiefly with Finland.

The coleopteran fauna has been insufficiently explored.

The entire carabid fauna of the three outer islands considered here comprises 77 species (Table 9). However, since they have not been treated separately in Tables 9–14 it is advisable at this stage, for purposes of comparison, to give an account of the functionally *macropterous* species of the three islands (Table 21). The functionally *brachypterous* species were listed above (under Hogland, Table 20), where the partially macropterous species, *Bembidion lampros*, *Calathus melanocephalus*, *Pterostichus minor* and *P. vernalis*, excluded from the present tabulation, were also considered.

270–271 **Table 21. Functionally macropterous (excluding dimorphic) species of three outer islands in the Gulf of Finland. Cf. Table 20 (p. 265)**

	Tytärsaari	Lavansaari	Seiskari	Also on Hogland
Acupalpus dorsalis	+	–	+	+
Agonum dolens	+	–	–	+
A. gracile	+	+	–	+
A. livens	–	–	+	+
A. mannerheimi	+	–	–	–
A. marginatum	+	+	+	+
A. sexpunctatum	+	+	+	+
A. viduum	–	+	–	+
Amara aenea	–	+	+	+
A. apricaria	+	+	+	–
A. equestris	–	–	+	–
A. famelica	–	+	–	+
A. familiaris	–	+	+	+
A. fulva	–	+	+	+
A. ingenua	–	–	+	–
A. majuscula	+	–	+	–
A. plebeja	+	–	–	+
Asaphidion pallipes	–	–	+	–
Badister dilatatus	+	–	–	+

	Tytärsaari	Lavansaari	Seiskari	Also on Hogland
B. peltatus	+	–	–	–
Bembidion andreae pol.	+	–	–	–
B. bipunctatum	+	–	+	+
B. doris	+	–	+	+
B. gilvipes	–	–	+	+
B. obliquum	+	+	+	+
B. quadrimaculatum	+	+	+	+
B. rupestre	+	+	+	+
B. saxatile	+	+	+	+
B. transparcus	+	–	–	+
B. velox	–	+	+	–
Blethisa multipunctata	+	–	–	+
Bradycellus collaris	+	–	–	–
Cicindela campestris	–	+	–	–
C. hybrida	–	–	+	–
C. maritima	+	+	+	–
C. silvatica	+	–	+	+
Clivina fossor	–	–	+	+
Dromius agilis	+	–	–	+
D. fenestratus	+	–	–	–
D. quadraticollis	+	–	–	–
Dyschirius obscurus	+	–	–	–
D. politus	–	–	+	–
D. thoracicus	+	+	+	–
Elaphrus cupreus	+	+	–	–
E. riparius	+	+	–	+
Harpalus aeneus	+	+	+	+
H. calceatus	+	–	–	–
H. griseus	+	–	+	–
H. latus	–	–	+	+
H. pubescens	+	+	+	+
H. quadripunctatus	–	+	–	+
Loricera pilicornis	+	–	–	+
Micolestes minutulus	+	–	–	–
Pterostichus aterrimus	–	–	+	+
P. niger	+	–	+	+
P. nigrita	+	+	+	+
P. oblongopunctatus	–	+	–	+
Stenolophus mixtus	+	–	–	–
Synuchus nivalis	+	–	–	–
Trechus quadristriatus	+	–	+	–
Trichocellus placidus	+	–	–	+

271 As already indicated (p. 266), the comparison in Table 21 shows that there are more species common to all the islands which are capable of flight
272 than the flightless species. Among the latter form *Pterostichus diligens* is the only exception. This can be expressed numerically by giving the mean occur-

rence of species capable of flight and of flightless species found on the three islands:

The 13 functionally brachypterous species are found on 1.46 islands; the 63 functionally macropterous species are found on 1.60 islands.

Dispersal of the flightless species depends mostly on coincidence and *time*.

Besides the discussion given for Hogland concerning the immigration of flightless species to these isolated islands it may be remarked that this element on the remaining three outer islands *shows no preponderance of larval hibernators* (Table 13). It is therefore possible that in this case transport with drift ice in spring has played a greater role. In this connection it is interesting to note that recent transport of bolders by ice from Lavansaari to Tytärsaari has been assumed (Rosberg, 1898, p. 4).

But the chief characteristic of the carabid fauna of these three islands is the pronounced dominance of species capable of flight (Tables 9–11). Of all the Fennoscandian islands considered only Gotska Sandön matches these islands in this respect, with an even higher percentage (Table 12, first column). If the outer islands are considered separately we find *the highest percentage of functionally macropterous carabids—the most in all of Fennoscandia—in Seiskari, with 87.5%*. Of all the Fennoscandian islands treated here only Hailuoto is younger!

In addition to the age, the excellent exposure between the two regions of mainland situated not far apart has also played a role in the relatively strong colonization by anemochorous species. From time to time similar events may also have taken place along the shores of the outer islands, as reported in the vivid description given by Palmén (1944) about insects washed ashore on the south coast of Finland.

Actually some of the carabids discovered on the outer islands bear the undisputed character of accidental migrants. These include the internationally notorius "migrants" ("Zugvögel"), such as *Bembidion transparens*, **Harpalus calceatus*,**H. griseus*, **Pterostichus aterrimus*, and possibly also *Agonum mannerheimi*, *Amara majuscula* and **Dromius quadraticollis*. In other cases the same conclusion can be drawn on the basis of the non-availability of any essential conditions for life on these islands for the species concerned, for example,
273 *Agonum dolens*, *A. livens*, *Badister dilatatus*, *B. peltatus*, and **Stenolophus mixtus*. The species with an asterisk must have come from the south, but *Agonum mannerheimi* (and certainly other species, not ascertainable more precisely) from the Finnish mainland.

6. Valamo

Unfortunately this is the only fresh water island of the region whose fauna has been reasonably well explored. Otherwise it would have been interesting to draw a comparison with Visingsö in Vättern, for instance, but on this island there has been almost no collecting activity.

The main island of Valamo, which alone is considered here, is barely 10 km long and has a surface of around 25 km^2 (Nielsen, 1897; Rosberg et al., 1923). The distance from the nearest mainland (south of Kl Sortavala) is 23 km; to the east (Kl Salmi) it is 27 km. The island is mountainous (Diabas) and richly wooded (chiefly with mixed forest). The highest point is 66 m above sea level, which must have already emerged from the sea in the Yoldia period (Sauramo, 1942, maps on pp. 227–228). There are several small lakes. The rich flora in the vicinity of the monastery shows considerable cultivation (including plantations); there is extensive cultivation of garden plants and vegetables. There are many horses and cattle.

Greek Catholic monks, now numbering about 500—representing the entire population of the Valamo islands*—are said to have colonized the islands as early as the end of the 10th century. There has always been brisk traffic with the adjacent mainland (chiefly with Sortavala in the past century). Ships can dock at the pier without transhipment.

The carabid fauna has in no way been exhaustively explored, but according to our present knowledge includes 59 species, and is therefore not particularly poor. Ecologically it shows a slight deficit of xerophilous species and a preponderance of forest species, more than on any other island of the region (Table 14). Among the dynamic groups (Tables 10, 12) *the preponderance of functionally brachypterous species is greater than on any of the Baltic Sea islands.* One might be inclined to look for the explanation in the age-old cultivation of the island, and to surmise that this element arrived chiefly anthropochorously.
274 However, this assumption is contradicted mainly by the above-mentioned preponderance of forest species. Moreover, among the brachypterous forms there are only three species that are anthropophilous to some extent (*Bembidion lampros*, *Patrobus atrorufus*, *Pterostichus vulgaris*). On the other hand *Bembidion ustulatum*, *Carabus nemoralis* and *C. cancellatus* are missing, in spite of the fact that the first two of these are more favored by culture and are all found in the region of comparison (6a) and even in Sortavala, a city with which Valamo had very active traffic in recent centuries.

Among the brachypterous forms there is a great preponderance of species that hibernate as larvae (Table 13); in the Baltic Sea area only Gotska Sandön shows a higher figure. In line with the discussion of the Skärgård of southwestern Finland, to a still greater extent this can be considered as evidence for the *great importance of hydrochorous transport in summer*. This assumption is supported by the short distance from the northern shore of Ladoga and the direction of the "monsoon winds" which are still favorable in early summer (Johansson, 1910, p. 28). It is uncertain whether in addition transport by inland fresh water is tolerated by the animals better than in the Gulf of Finland (saline content up to 6‰; see map in Fig. 79, p. 518). The experiments by

*Conditions have changed during the war.

Palmén (1944, p. 155) with different Coleoptera, including 7 carabids, show no disadvantageous effect of water of such low saline content.

7. Värmdön (and Djurö)

This is the largest island of the Skärgård of Stockholm, including Ingarö Island which has now merged with it. It is more than 250 km² in surface. Värmdön is much fragmented, with numerous deeply incised bays. In the west it is separated from the mainland at the narrowest point of Skurusund strait, which is only 60 m wide. Since 1832 there was a floating bridge at this place, replaced in 1915 by a broad modern concrete bridge. In the north the farthest headland is 4 km away from the mainland. The sea all around is full of islands and skerries. —In the following account little Djurö Island, situated less than 1 km east of Värmdön, is also considered since it contains different, sandy biotopes and has been somewhat better explored.

The highest point (NE of Kilsviken) is 71 m above sea level; in the north a height of 59 m above sea level is attained. These points emerged from the sea only at the beginning of the Littorina period (see maps in Munthe, 1940, and Sauramo, 1942, p. 241; Almquist, 1937, p. XXXVIII).

275 The population is dense, comprising 7,000 to 8,000 people. In addition there are thousands of summer visitors from Stockholm. The traffic with Stockholm is very active, and has greatly increased during the last 30 years by the overland route (automobiles).

The region is very rich in biotopes. There is rocky ground (basement complex) as well as moraine and fertile loamy soil and, especially in Djurö, sand. There is no firm limestone outcropping. There are numerous small lakes, swamps and bogs, although the latter have been largely drained. However, forest occupies the largest area, chiefly coniferous forest, but there are also mixed deciduous forests and luxuriant groves. The meadow vegetation and the flora in general are strikingly rich (Stockholmstraktens Växter, 1937). The seashores are usually rocky, clayey in the bays and in Djurö there are sandyshores, but no quicksand.

There is no comprehensive study of the coleopteran fauna available, and its exploration cannot be considered exhaustive. Nevertheless 104 species of carabids are known from the region (Table 9).

Ecologically the fauna shows a slight deficit of xerophilous species and some preponderance of forest species (Table 14). The proportion of the functionally brachypterous species is perceptibly larger than in the region of comparison (Tables 10, 12). The relationship between larval and imago hibernators (Table 13) is distinctly positive.

In conclusion it may be stated that the carabids of Värmdön constitute a less extreme fauna, which largely corresponds with that of the region of comparison with respect to its ecologic, dynamic and life history parameters. Crossing the narrow straits has apparently not posed any great difficulty even

to flightless species. It is probable that anthropochorous dispersal has also taken place. Of the 9 brachypterous or functionally dimorphic species of the region of comparison, which can be considered at least more or less equally anthropophilous, only two are lacking in Värmdön: *Pristonychus terricola* and *Stomis pumicatus*, which occur very sporadically in central Sweden.

The fauna of the insular region on the whole is identical as well with that of the mainland region of comparison. There are only two species, *Dromius linearis* and *Harpalus calceatus*, not found there. Of these, *Dromius* is an exclusively coastal beetle in this part of its area, and *Harpalus* is an accidental immigrant. Otherwise there is no other basis for the assumption that the fauna of Värmdön–Djurö immigrated from a different direction than from the nearest mainland.

276 **8. Ösel and Dagö**

These two islands can be dealt with only cursorily, partly because their fauna (especially that of Dagö) is not very well known, and primarily because it was impossible for me to obtain voucher specimens of the dimorphic species for examination. Hence the dynamic character of the fauna could not be determined more precisely. This is regrettable all the more since a detailed comparison with the islands Gotska and Öland, which are similar in many respects, would have been of great interest.

Dagö (Hiiumaa) has a surface of 965 km^2. The distance from Ösel is only 4.3 km and from the mainland coast in the east 25 km; however, the island of Ormsö (Vormsi) lies in this strait. The population (about 17,000) came largely from Estonia but in olden times colonization also took place from Sweden (Gotland?).

Ösel (Saaremaa) has a surface of 2,618 km^2. The distance from the mainland of Estonia in the east is scarcely 20 km (the strait contains the large island Moon); the farthest mainland of the Sworbe Peninsula in the south is about 30 km away from the north coast of Kurland. The population (about 60,000 people) came from Estonia.

The natural conditions of the two islands are very much identical. They are the remains of a low, horizontal plateau region, which consists of Cambro-Silurian, chiefly limestone rock, and is partly covered with moraine. The highest point in Dagö is about 60 m above sea level, and in Ösel about 50 m above sea level. The oldest parts of the two islands emerged from the sea at the end of the Yoldia period (Sauramo, 1942, map on p. 231). It is therefore not surprising that fossils of an Arctic flora have not been found on these islands (Kupffer, 1925, p. 163). The recent occurrence of *Pinguicula alpina* (l.c., p. 164) in Ösel, and in Gotland, is all the more striking. No land corridor with the mainland or other islands seems to have existed since the last glaciation in spite of the shallow strait (< 20 m) separating the two. On the contrary, during the Littorian rise of the land ("Transgression") the surface of the islands was

Table 22: Species absent from Ösel–Dagö but found in Gotland and Öland. Species in parentheses are missing from the entire eastern Baltic.

E—Occurring on the mainland of Estonia; xt—more or less pronounced xerophilous and thermophilous species; b—Brachypterous species or dimorphic species occurring in Öld–Gtl in brachypterous form.

E	*Acupalpus consputus*
	A. exiguus
E	*A. flavicollis*
E	*A. meridianus*
E	*Agonum dorsale* xt
E	*A. gracile*
E	*A. krynicki*
E	*A. livens*
E	*A. piceum*
E	*A. ruficorne*
E	*A. viduum*
E	*Amara brunnea*
	(*A. convexiuscula*)
E	*A. equestris*
E	*A. famelica*
E	*A. ingenua*
	A. lucida
E	*A. lunicollis*
E	*A. nitida*
E	*A. ovata*
E	*A. praetermissa*
E	*A. quenseli*
E	*A. similata*
E	*A. tibialis*
E	*Anisodactylus binotatus*
E	*Badister unipustulatus*
E	*Bembidion articulatum*
	(*B. Clarki*) b
E	*B. dentellum*
E	*B. gilvipes* b
	B. pallidipenne
E	*B. quinquestriatum*
E	*B. rupestre*
E	*B. unicolor* b
E	*Blethisa multipunctata*
E	*Brachynus crepitans* xt
E	*Bradycellus collaris* b
E	*Calathus mollis* xt, b
E	*Carabus violaceus* b
E	*Chlaenius tristis*
E	*Cymindis angularis* xt, b
	(*C. humeralis*) xt, b
	(*Demetrias monostigma*)
	(*Dichirotrichus pubescens*)
E	*Dromius agilis*
E	*Dromius fenestratus*
	D. linearis xt, b
E	*D. marginellus*
E	*Dyschirius politus*
E	*Harpalus anxius* xt
	(*H. azureus*) xt, b
E	*H. griseus*
E	*H. hirtipes* xt
	(*H. melancholicus*) xt
	(*H. melleti*) xt
E	*H. quadripunctatus*
E	*H. rubripes* xt
	(*H. rupicola*) xt
	(*H. serripes*) xt
	H. vernalis xt, b
E	*Lebia crux-minor*
E	*Masoreus wetterhalli* xt, b
	Nebria brevicollis
	(*N. salina*)
E	*Pterostichus aterrimus*
E	*P. diligens* b
E	*P. gracilis*
E	*P. minor* b
E	*P. punctulatus* xt
E	*P. strenuus* b
	(*Trechus obtusus*) b
E	*Trichocellus cognatus*
E	*T. placidus*

again much reduced (Munthe, 1942, Plate XIV).

The higher *flora* of Ösel and Dagö has not been investigated thoroughly, but a remarkable conformity with that of Gotland–Öland is evident (Skotsberg and Vestergren, 1901; Kupffer, 1925; Eklund, 1928). It is strikingly rich especially in Ösel, comprising about 900 species (Kupffer, p. 111). In the concluding section of the Baltic islands (p. 298) some general remarks concerning the flora are given.

277 The *coleopteran fauna* of the two islands is not completely known (in addition to the literature cited in Part I, see von Szeliga–Mierzeyewski, 1942), particularly on Dagö. But even from Ösel there are no records of species like *Agonum viduum*, *Amara similata*, *Bembidion rupestre*, *Dromius agilis*, *Pterostichus diligens*, *P. minor*, *P. strenuus*, and *Trichocellus placidus*, which should not be absent there.

But we may be justified in drawing a comparison with the fauna of Öland and Gotland (excluding Fårön and Gotska Sandön). It is small wonder that the number of carabids unknown in Ösel–Dagö but found in Öland and (or) Gotland is as high as 114.

If we restrict ourselves to species that *occur both in Öland and Gotland*, and leave out certain critical species some of which arrived late (*Agonum moestum*, *Amara cursitans*, *A. littorea*, *A. majuscula*, *Badister dilatatus*, *Dyschirius aeneus*) then 73 species are left that are not known in Ösel–Dagö (Table 22).

278 This list contains numerous "trivial" species whose discovery in Ösel-Dagö, as mentioned above, is only a question of time. Besides, there are many animals especially characteristic of Öland–Gotland, some of which are conspicuous and easy to collect, and belong to the *xerophilous-thermophilous* faunal element of Öland–Gotland (xt above; 17 species). As long as they are completely missing from the Baltics (6 species) this is understandable, probably owing to their history of immigration. But no fewer than 9 species occur even on the Estonian mainland. Of the 17 species, 7 are constantly brachypterous or dimorphic (in Öland–Gotland also occurring in the brachypterous form;
279 see Tables 9, 11) and thus represent an element that has difficulty dispersing ("schwerverbreitetes Element").

In contrast with the above list of 73 species there are only 12 species of the fauna of Ösel–Dagö which are not found in Öland–Gotland:

*Agonum micans**
Amara spreta
Asaphidion pallipes
Bembidion andreae polonicum
B. argenteolum
B. azurescens
B. litorale
Carabus arvensis
C. convexus
Cicindela maritima
Harpalus distinguendus
Sphodrus leucophthalmus.

*Published as "*Europhilus scitulus* Dej." (von Szeliga-Mierzeyewski, 1942, p. 185), but supposedly identical with *Agonum micans.*

Sphodrus is anthropobiont. Of the remaining species only 3 (*Agonum micans*, *Carabus arvensis* and *Harpalus distinguendus*) occur in the Swedish regions of comparison (11a, 12a) of Gotland and Öland. The possibilities of immigration may have been lacking to the others.

We therefore find a fundamental difference between the carabid faunas of Ösel-Dagö and Öland-Gotland, such that the former region lacks just the species characteristic of the latter region. Concerning the presumable causes, reference may be made to the concluding section on the Baltic islands (p. 298).

9. Gotska Sandön

In many ways this island is the most interesting one in the entire Fennoscandian region. Its coleopteran fauna includes many species unknown in the rest of northern Europe. Their origin is very disputed (Mjöberg, 1912; Ekman, 1922, pp. 429 ff.; Jansson, 1925; see also Engström, 1926; Bengt Pettersson, 1946).

The shape of the island is almost rhombic and the surface 36 km^2. The distance from Gotland is 50 km and from the most northern coast of Fårön Island 38 km. The nearest point on the Swedish mainland (Sdm) is about 90 km away, Ösel about 150 km, and the coast of Kurland about 170 km. This is therefore the most isolated of all the Fennoscandian islands.

There are no rock outcrops. The island is chiefly made of sand, which is generally so fine that along the coast, once also in the inland, it has produced
280 massive shifting dunes consisting of quicksand. There is an unceasing struggle between forest and sand, and the numerous dead, half-buried plants show that this has not always resulted in the victory of the former. At some places, especially along the south coast, there is coarse gravel and rubble.

The interior of the island is almost all wooded. As a consequence of dryness and paucity of nutriment the ground is generally very sparsely covered, with *Calluna*, *Cladonia*, etc. A richer vegetation occurs mainly in the interspersed regions of deciduous forest primarily in the "great deciduous forest" in the northwest, which consists chiefly of the majestic *Corylus*, in addition to *Quercus*, *Betula*, *Populus tremula*. Due to extensive humus formation the soil here is rich in vegetation. —There are no bodies of open fresh water on the island.

The highest point, situated in "Höga Åsen" in the north, is 42 m above sea level. This must mean that the first sandy shore of the present Gotska Sandön emerged from the sea only *at the beginning of the Littorina period.* The island was unaffected by the earlier regressions, thus Mjörberg's opinion (1912, p. 188), that the fauna immigrated from Gotland over a "land corridor" is erroneous (cf. also V. Hofsten, 1920, p. 51; Lundblad, 1921).

Traces of human activity on Gotska Sandön go back to the Old Stone Age when the island had just emerged. However, the population has always been very sparse since the soil is not very suitable for agriculture. There are

remains of an old farm with small abandoned tilled regions in the southwest. At present only a little more than 20 people live on the island, all being staff of the lighthouse in the northwest. From time to time up to 60 forest workers are lodged in the barracks in the southern part of the island (Arwidsson, 1938, p. 6). —At any rate the influence of man on the flora and fauna of the island has to be judged as very low. Even small ships cannot be docked and all freight must be transhipped and landed in small boats. However in medieval times a harbor apparently existed on the east coast of the island (Engström, 1926, pp. 69 ff.). It may also be noted that on account of the scarcity of grass, hay for the few domestic animals has to be imported from Gotland almost throughout the year (Jansson, 1925, p. 43). There have been repeated attempts to plant the dunes partly with imported plants (Bengt Pettersson, 1946, pp. 38–40).

281 A synopsis of the flora of Gotska Sandön is provided by Arwidsson (1938). Given the poverty of biotopes on the island, the flora may be considered almost rich, although a major component is undoubtedly anthropochorous. The flora lacks any peculiarities comparable with those of the Coleoptera mentioned below. The most interesting species is *Orobanche alba rubra*, whose occurrence is highest in northern Europe, although it also grows in Gotland and Öland.

Our knowledge of the *coleopteran fauna*, thanks to the various studies by Jansson, is almost exhaustive and includes about 615 species so far (Jansson, 1925; 1935; and *in litt.*). It is very interesting, mainly because, as mentioned above, it includes some species whose occurrence here is unique in northern Europe.

These are the following six species*:

Hymenorus doublieri Muls.**	*Rushia pareyssi* Muls.
Plegaderus haraldi A. Janss.	*Temnochila coerulea* Ol.
Pogonochaerus caroli Muls.	*Xanthochroa carniolica* Gistl.

All of them, at least in the larval stage, are asociated with *Pinus*.

Ninety species of *carabids* are known (Table 9) but none of them is strikingly peculiar or unexpected. With the exception of *Bradycellus similis* all are found in Gotland (including Fårön). This species may yet be discovered on the mainland, where only *Calluna* occurs.

The dynamic character of the carabid fauna is of the greatest interest. Of all the islands of Fennoscandia here considered, Gotska Sandön has the highest deficit in brachypterous species (Tables 10, 12). Only the outer islands (excluding Hogland) in the Gulf of Finland have almost as few brachypterous species, with fewest on Seiskari, the youngest of these islands (see p. 272). The occurrence of *Calathus mollis* exclusively and of *Dromius nigriventris* predomi-

*In Sweden the following species are exclusively found in Gotska Sandön and Fårön; *Atheta janssoni* Bernh., *Nacerda rufiventris* Scop., and *Pityopthorus pubescens* Mrsh. The first two are seashore species.

***Hymenorus* has also been found in Finland.

nantly in the macropterous form is characteristic, and not found elsewhere on these islands.

Because the number of functionally brachypterous species on Gotska
282 Sandön is so small, division of these into developmental biological groups (Table 13) and ecological groups (Table 14) is somewhat inaccurate. Of course in the former case the great preponderance of *larval hibernators* is striking (more than on any other Baltic Sea island), and among them the unrivaled predominance of *xerophilous* species.

The carabid fauna thus bears an unambiguous indication of very recent immigration. That this has taken place chiefly by air is evident not only from the large proportion of macropterous species and forms but also from the numerous species which have accidentally arrived by flight and for which the essential requirements for existence are lacking on the island, or which throughout our region represent transmigrating ("transgredierende") species. The following 25 carabids of Gotska Sandön may be considered as such "accidental migrants":

Acupalpus consputus
Agonum gracile
A. gracilipes
A. livens
A. piceum
A. sexpunctatum
A. thoreyi
Asaphidion flavipes
Badister dilatatus
B. peltatus
Bembidion articulatum
B. assimile
B. doris
B. guttula
B. obliquum
B. varium
Blethisa multipunctata
Chlaenius tristis
Elaphrus uliginosus
Harpalus calceatus
H. griseus
H. punctatulus
Loricera pilicornis
Pterostichus anthracinus
P. gracilis.

All of these are winged and may be considered as having arrived anemochorously (or anemohydrochorously, in Palmén's sense, 1944).

Such a recent arrival of insects washed ashore along the coast of Sandön was observed by Anton Jansson and Rapp in early July, 1946. I obtained a list of the following carabids from them:

Acupalpus consputus
A. dorsalis
Agonum gracilipes
Amara aenea
A. aulica
A. bifrons
A. majuscula
A. tibialis
Asaphidion flavipes
Badister dilatatus
Bembidion assimile
B. guttula
B. minimum
B. obliquum
B. quadrimaculatum
B. varium

B. velox
Calathus melanocephalus
283 *Dyschirius impunctipennis*
D. lüdersi
Harpalus griseus
H. seladon
H. tardus
Microlestes minutulus
Trechus quadristriatus.

Concerning the accidental occurrence of other anemochorously dispersed insects on the island, see Jansson, 1925 (pp. 40 ff.)

It is noticeable that all the species of insects found in Sweden only on Gotska Sandön (Jansson, 1935, p. 54)* are capable of flight and thus may have immigrated by air as well. Mjöberg's discussion (1912, pp. 184 ff.), with a list of insects capable of flight but too "weak" to tolerate transport by water to Gotska Sandön, is difficult to understand, as also the point of the experiments on exposure to water (l.c., p. 199) carried out with *Ergates faber*.

On the other hand, Jansson's (1925, p. 31) opinion that the southern species now occurring isolated on Gotska Sandön have immigrated anemochorously, in no way contradicts their *relict* character. In *which way* they immigrated does not matter in this context, only *that this must have taken place when the* (climatic) *conditions were different from today's* (during the postglacial warm period, probably in the Sub-boreal), *mainly because immigration is not possible today* on account of the long distance from the present main area (of distribution)† of the species concerned. The continued occurrence of these species of Gotska Sandön even after the climate deteriorated, when they apparently died out in neighboring regions (for instance, in Gotland and in the Baltics), is certainly due to microclimatic conditions which are characterized by the favorable thermal influence of the warm sand in summer, especially on fallen tree trunks, which are more or less covered with sand.

There is thus no justification for speaking of "secondary or pseudo-relicts" (Jansson, 1925, p. 31). It is my opinion on the whole, that the term "pseudo-
284 relict" (Ekman, 1922, p. 279), which is mostly applicable to fresh water animals (example: *Eurytemora lacustris*, Ekman, l.c., p. 302), can be dispensed with in the case of terrestrial fauna (Lindroth, 1943a, p. 140; see also p. 677 below).

It remains to explain the immigration to Gotska Sandön of species for which anemochorous dispersal is out of the question, the functionally brachypterous element of the carabid fauna. We have to determine the significance of transport by man as against that by water and ice.

With regard to Gotska Sandön the botanists are inclined to ascribe great

*However, *Deltocephalus thenii* Edw. should be excluded, since it is similar to *Psammotettix confinis* Dahlb. (Ossiannilsson, 1937, p. 20). Moreover *Bledius tibialis* Heer (Catalogue, 1939) and *Medon dilutus* Er. and *Pediacus dermestoides* Fbr. should be excluded: according to Jansson (*in litt.*) the determination of the two latter species is incorrect.

†(suppl. scient. edit.)

importance to anthropochorous dispersal: "The majority of species native to the island (or once native) undoubtedly arrived directly or indirectly as a result of cultivation by man" (Arwidsson, 1938, p. 19; translated from the Swedish into German). In view of the occurrence of numerous "weeds" found in patches, for instance at "Gamla gården" (= old farm), this view is probably correct (and hence expressible in terms of species statistics). But when we consider only the species of plants not pronouncedly synanthropous the contention seems to be greatly exaggerated. I am referring to the 100 percent occurrence of the Swedish species of *Pyrola* on Gotska Sandön, as well as the rich occurrence of orchids, some in very unusual habitats, and *Orobanche alba rubra*, whose presence must be explained by effective anemochorous transport; and likewise the completeness of the species of *Sorbus* and *Crataegus* (all according to Arwidsson, 1938), whose occurrence is largely the result of endochorous dispersal by birds.

In spite of the cultivation, partly of imported plants*, undertaken for the purpose of sand dune consolidation, as well as the regular import of hay, Gotska Sandön is undoubtedly to be considered as *comparatively unaffected* by culture (Bengt Pettersson, 1946, p. 45). The carabid fauna seems to confirm this view. Of the 8 functionally brachypterous carabids (*Bembidion lampros*, *B. obtusum*, *B. ustulatum*, *Calathus fuscipes*, *Carabus memoralis*, *Patrobus atrorufus*, *Pristonychus terricola*, *Pterostichus vulgaris*) occurring in Gotland (and the surrounding small islands), which are more or less favored by culture, only *Calathus* occurs on Gotska Sandön; in contrast 6 of them (with the exception of *Bembidion ustulatum* and *Pristonychus*) are found in Fårön.

We are justified in concluding that anthropochorous transport of carabids
285 to Gotska Sandön was of minor importance, and that the flightless species in question reached the island predominantly by hydrochorous dispersal. The strikingly large number of larval hibernators among these species (Table 13) justifies the supposition that this immigration has taken place in *summer* and not with drift ice. —The significance of the "Baltic drift" for the dispersal of plants, among other to Gotska Sandön, has already been recognized by Sernander (1901, pp. 138 ff.). Unfortunately we still have so little knowledge of the surface currents of the Baltic Sea (as far as I am aware there is no map, but reference may be made to Fig. 19, p. 247) that no conclusion can be drawn as to the most probable direction from which transport to Gotska Sandön took place. Yet it appears that the currents in the eastern Baltic Sea are directed mainly *north*, and in the western Baltic Sea *south* (cf. salinity map, Fig. 79, p. 518), so that transport of "southern" species is favored from the *east*.

The astonishingly high number of Coleoptera found on Gotska Sandön results from two things: on the one hand the eminent success of assiduous col-

*However, according to Bengt Pettersson (1946, p. 40) *Lathyrus maritimus*, for instance, is indigenous to Gotska Sandön (but cf. Arwidsson, 1938, pp. 22, 53).

lecting by one man (Anton Jansson), and on the other the immense importance of anemochorous (including anemohydrochorous) transport for the dispersal of winged insects.

10. Fårön

This island is situated immediately NE of Gotland, separated only by a strait about 500 m broad at the narrowest point. The distance from the nearest mainland (Södermanland) is 125 km, from the coast of Kurland 140 km. The surface is more than 110 km^2. The highest point, lying in the west, is only 28.1 m above sea level (Munthe, Hede, Lundqvist, 1936). According to Munthe (1940, Plates X, XII) the island emerged during the Ancylus period, only to be submerged later due to rise in sea level ("Transgression"). Permanent existence was attained only during the Littorina period, after the sea receded subsequent to submergence (about 6,500 years ago) by a gradual amalgamation of several islets forming the present-day Fårön. In spite of the small depth of Fårösund strait (only 5.5 m at the northern entry) the island may never have possessed a firm land corridor to the mainland.

The population is only about 1,000 people, and large regions are uncultivated. The traffic is exclusively via the Fårösund strait, across which a ferryboat now carries even large vehicles.

286 The landscape is poor and dry, and is chiefly made of limestone rocks and calcareous shore gravels of all sizes. In the east there is an extensive quicksand area, Ulla Hau, which apparently is comparatively young (Jansson, 1925, p. 36). On account of the continuous emergence of land (at present about 25 cm in 100 years) many former bays have been transformed into shallow lakes.

In spite of the uniform subsoil composition there is a fairly large variety of biotopes (Durango, 1946). The open pine (*Pinus*) forest is dominant but there are also rich meadows of leaves ("Laubwiesen") juxtaposed with unforested Alvar[†] regions. The shores, particularly of the fresh waters, are amazingly variable. The flora is typical of Gotland, even though the species are fewer (K. Johansson, 1897).

The *coleopteran fauna* has not been studied as thoroughly as that of Gotska Sandön—the only synopsis is Mjöberg's (1905)—but our current knowledge shows that it is considerably richer. There are 134 known species of carabids. With respect to dynamics the fauna shows a distinct deficit of functionally brachypterous species (Table 12, last column), which, however, is much smaller than that of Gotska Sandön. In this respect Fårön is intermediate between this island and Gotland. The same is true of the larval hibernators, which are also preponderant in Fårön (Table 13). Among all the islands considered, ecologically (Table 14) the dominance of xerophilous species is greatest after Gotska

[†](Plant community consisting typically of mosses and calciphilous herbaceous plants that grow on steppelike shallow alkaline soils overlying Scandinavian limestones; suppl. scient. edit.).

Sandön and the deficit in forest species is similar to the latter island.

Species in the fauna of Fårön not found on the main island of Gotland are of special interest. These are the following 11 species:

Agonum gracilipes
Bembidion andreae polonicum
B. octomaculatum
B. transparens
Bradycellus harpalinus
Carabus clathratus
Cymindis macularis
Demetrias imperialis
Dyschirius impunctipennis
Harpalus calceatus
Nebria livida.

Of these species 8 are constantly macropterous and capable of flight, 3 (*Bembidion transparens, Carabus* and *Cymindis*) are dimorphic. Among these *Bembidion transparens* is found in Fårön only in macropterous form, the other two (known from one and two specimens respectively) only in brachypterous form (Table 11). Some of the functionally macropterous species (*Agonum*
287 *gracilipes*, *Bembidion octomaculatum*, *B. transparens*, *Harpalus calceatus*) are notorious "migrants" ("Zugvögel"), and *Demetrias imperialis* was found on the seashore, certainly an accidental occurrence. A clue to the direction of immigration is provided by *Bembidion andreae*, for this species could have arrived only from the east (see map in Part II).

Elsewhere, too, the two functionally brachypterous species were found to have dispersed with astonishing ease, *Carabus* primarily to the islands in Kvarken (Gulf of Bothinia; see p. 381), *Cymindis* to Åland and the Skärgård east of it (see p. 248), and to Sandön (Sandhamn) in the outermost Skärgård of Stockholm. In all probability they reached Fårön by hydrochorous transport (both occur in Kurland).

The following two observations show how the fauna of Fårön, at least temporarily, can be enriched by wind drift (possibly with hydrochorous transport as the final phase):

1. Palm (in litt.; cf. also Palm, 1947a, p. 44; 1947b, pp. 171, 177) found large quantities of Coleoptera on June 16 and 17, 1946 on the barren, sandy seashore at Ava in the eastern part of the island. The carabids were represented by the following species:

Acupalpus dorsalis, numerous specimens
A. exiguus, 5 specimens
A. meridianus, numerous specimens
Agonum gracilipes, 4 specimens
(*A. marginatum*, numerous specimens)
A. piceum, 1 specimen
A. sexpunctatum, 1 specimen
Amara apricaria, 1 specimen
A. familiaris, numerous specimens
(*A. quenseli*, numerous specimens)
A. tibialis, numerous specimens
d (*Bembidion assimile*, numerous specimens)
d *Bembidion lampros*,

numerous specimens
B. minimum, numerous specimens
B. obtusum, 2 specimens
(*B. pallidipenne*, 4 specimens)
d *B. properans*, 1 specimen
d *B. transparens*, 1 specimen
Dyschirius aeneus, 1 specimen
D. lüdersi, numerous specimens
(*D. obscurus*, numerous specimens)
D. politus, 1 specimen
(*D. thoracicus*, numerous specimens)
Harpalus luteicornis, 1 specimen
Microlestes minutulus, numerous specimens
Odacantha melanura, 2 specimens

The species in parentheses may be native to the biotope, the others must have immigrated. All these animals were macropterous, including 5 species of *Bembidion* which are otherwise dimorphic ("d").

The following are exclusive records from Fårön: *Acupalpus exiguus*, *Bembidion minimum*, *B. obtusum*, *B. properans*, *Dyschirius aeneus*, *D. politus*, and *Odacantha*. Also represented in this material were *Hylastes attenuatus* Er.
288 (Palm, 1947a, p. 44), which is new for Sweden, and *Gronops inaequalis* Boh., which recently immigrated into Fennoscandia from the east (Har. Lindberg, 1942; Palmén, 1945c; Nyman, 1946; Palm, 1947b, p. 177). The drift material of carabids also included two species (*Agonum gracilipes* and *Bembidion transparens*) previously not found in Gotland, and two other species extremely rare in Gotland or occurring only sporadically: *Harpalus luteicornis* (only one specimen at the Fårösund strait) and *Odacantha* (2 localities). —*The area where this drift originated cannot be the main island of Gotland.*

2. The second observation of insect drift was made on May 9, 1948 by N. Höglund, and G. Notini on the northern side of Ulla-Hau, i.e., on the shore of Ekeviken in the eastern part of the island. The days before had been warm and still, but then a strong north-easterly wind set in. On this particular day the otherwise barren sandy beach facing north was densely occupied along the watermark by insects, chiefly Coleoptera, evidently brought there by the combined action of wind and waves, anemohydrochorously.

I obtained the entire unmounted material of Coleoptera for study. It was quite rich in individuals, less so in species, and included the following carabids:

Acupalpus consputus, 2 specimens
A. dorsalis, 33 specimens
Agonum piceum, 4 specimens
Badister dilatatus, 1 specimen
Bembidion doris, 9 specimens
d *B. guttula*, 2 specimens
B. obliquum, 93 specimens
B. quadrimaculatum, 51 specimens
B. varium, 2 specimens
Dyschirius ludersi, 1 specimen
D. politus, 1 specimen
Loricera pilicornis, 1 specimen
Trichocellus placidus, 2 specimens

All the individuals are macropterous, including the two specimens of the dimorphic species *Bembidion guttula*.

Three species (*Acupalpus consputus*, *Badister dilatatus* and *Trichocellus placidus*) were new to Fårön; it may thus be assumed that the point of origin

of the drift was distant. The fact that *Hylastes attenuatus* discovered by Palm (see above) was also represented here by one individual is an indication that in this case too the animals came from the east.

The fauna of Fårön has obtained a large share of its insect species by anemochorous (and anemohydrochorous) transport from the eastern Baltics and continues to receive new additions by this route. The discovery resulting from the
289 study of Åland, that this transport in the Baltic Sea region takes place chiefly *from east to west*, is thus confirmed. It also holds for Gotska Sandön. How far the fauna of the main island of Gotland has been enriched in this way will be discussed below.

11. Gotland

Only the main island is considered here. The Karlsöarna are excluded as well; their insect fauna is too little known.

Gotland measures 2,960 km^2 and is 135 km long. The shortest distance from the Swedish coast (Småland) is about 90 km. It is about 150 km to Kurland and more than 170 km to Ösel. Öland lies about 70 km away. The highest point (Lojsta) is 83 m above sea level.

When the last inland ice was melting away†, Gotland was completely covered by the sea, but the highest parts had already emerged in the early phase of the Baltic ice sea period (Munthe, 1940, Plate II; Sauramo, 1942, p. 227). During the first part of the Yoldia period, Arctic plants like *Dryas* and *Salix "polaris"* immigrated, and with the transition to the Ancylus period not only *Pinus* but also *Cladium* and *Corylus* arrived (Munthe, l.c., pp. 66–67, 71, Plate VII, Diagram 8). The land emergence was at first very rapid and at the beginning of the Ancylus period the island's surface in the south must have been greater than at present. Munthe (1910, pp. 34–41; 1911, p. 356) believed that at this time a direct land corridor with North Germany was "highly probable," but later he posits only a series of islands, including some large ones, in the southern Baltic Sea (1940, Plates II, IV, X, XI). Below we will return to these questions, which are important for the possibilities of immigration of fauna.

To the Swedish "mainlander" nature in Gotland does not appear as peculiar as on Öland. All types of biotopes occurring on this island are also represented in Gotland, however, they occur only rarely in such rough contrast with one another as the "Alvar" and the luxuriant groves south of Borgholm. But the widespread open pine forests of the island of Gotland impart to it a more commonplace appearance.

Above sea level Gotland is made up entirely of Upper Silurian rocks, chiefly limestone rock or marl, and in the extreme south sandstone as well (Munthe and Lohmander, 1946, map on p. 15). Mostly the rocky ground is covered with strongly argillaceous moraine and in the lower regions, especially close to the coast, also with loam, sand or gravel later carried down to the

†(At the end of the last glaciation; suppl. scient. edit.).

sea. Nevertheless in all parts of the island there also occur barren, true Alvar[†]
290 regions. Their frequent aridity in summer is due not only to their fissured structure but also to the low precipitation over the island.

However, about 40% of the surface area is wooded, chiefly with *Pinus*; the famed meadows of leaves ("Laubwiesen") (Gottlandish plural "ängen") have unfortunately diminished in recent decades (Stenström and Romell, 1945; Bengt Pettersson, 1946, pp. 165 ff.). The moors ("myrar"), characterized especially by *Cladium*, originally occupied at least 10% of the surface but they have mostly been drained and were possibly transformed into arable soil, so that not even one-tenth remained untouched. Linemyr in the east is the largest such region (B. Pettersson, l.c., pp. 178 ff.). There are shallow lakes, especially in the north, mostly with barren shores. —The coast is frequently steep, especially in the west, and the sea has fashioned the well-known "hedge mustard"[††] ("Rauke") from the rock columns. Usually there is a more or less broad belt of rubble, gravel or sand along the shore. True quicksand is rare.

The colonization of Gotland by man took place early (Munthe, 1940, pp. 160, 164–165), probably during the last part of the Ancylus period (7,500 to 8,000 years ago). The present population is about 57,500. More than one-fourth of the land surface is cultivated. Sea traffic is chiefly with Stockholm. During the Viking period and later Gotland was a cultural and trade center for the entire Baltic Sea region.

The *flora* of Gotland is extremely rich and long known for its "rarities." The following 11 vascular plants ("large species") of Sweden occur only in Gotland (including the adjoining small islands):

Arabis nemorensis
Calamagrostis varia
Cephalanthera alba
Euphrasia salisburgensis
Lactuca quercina
Orchis palustris
O. spizelii
Ranunculus ophioglossifolius
Sanguisorba officinalis
Tofieldia calyculata
Tragopogon crocifolius.

Sixteen Swedish species are restricted to Gotland and Öland, as mentioned below (p. 299).

The *coleopteran fauna* of Gotland is correspondingly rich, and many species discussed below (p. 303) are otherwise not known in Sweden or even northern Europe. Among the carabids, 195 species have so far been found on the main island (Table 9), i.e., almost 54% of the entire Fennoscandian fauna.
291 None of the species in our region is restricted to Gotland, but the following species in Scandinavia occur only in Öland and Gotland: *Harpalus azureus*, *H. punctatulus*, and *H. rupicola*.

[†] (cf. p. 285; suppl. scient. edit.).
[††] (supposedly *Eureka sativa*; suppl. scient. edit.).

With regard to the dynamics (Tables 10, 12), as well as the hibernation types (Table 13) the composition of the carabid fauna is almost exactly as in the two regions of comparison on both sides of the Baltic Sea. It is thus considered "normal." Ecologically (Table 14), especially in comparison with Öland, it shows a striking deficit of xerophilous species and almost likewise, a distinct deficit of forest species. The former is strengthened by the occurrence of a significant number of more or less sporadically occurring *macropterous* hygrophilous species, which have immigrated from the east.

In the above treatment of the Fårö-fauna we found a number of species capable of flight, which seemed to be immigrants (some of them accidental) from the eastern Baltics. Among the carabid fauna of the main island it is striking that quite a few species, so far as is known, are restricted to the east coast (up to 10 km inland). The following 17 species are to be taken into consideration:

Agonum krynicki
A. piceum
Amara famelica
A. plebeja
Anisodactylus binotatus
Bembidion dentellum
B. humerale
Blethisa multipunctata
Demetrias monostigma
Dromius fenestratus
D. quadrinotatus
Elaphrus uliginosus
Harpalus griseus
H. luteicornis
Oodes helopioides
Trechus obtusus
Trichocellus cognatus.

In contrast there are 12 species found only on the west coast of Gotland:

Agonum ruficorne
Amara cursitans
A. majuscula
A. nitida
Bembidion velox
Broscus cephalotes
Carabus glabratus
Dichirotrichus pubescens
Dromius angustus
Dyschirius obscurus
Harpalus vernalis
Nebria gyllenhali.

The dissimilar *ecological* character of the two groups of species must strike every coleopterist going through the above lists. The eastern group includes predominantly *fresh-water hygrophilous species,* i.e. 10 species = 59% (cf. Table 9). In the western group there are 5 hygrophilous species (= 42%) but they are *all seashore species.*

292 With regard to dynamics the eastern group includes 2 functionally brachypterous species (*Demetrias monostigma, Trechus obtusus* = 12%), the western group includes 3 species (*Broscus, Carabus glabratus, Harpalus vernalis* = 25%). The two first-mentioned species are missing in the Baltics*, but *all of the remaining members of the eastern group occur in the eastern Baltics,*

*The old record of *Trechus obtusus* from Kurland is undoubtedly erroneous (see Part I).

*even in Kurland**. In the western group two-winged species (*Dichirotrichus pubescens*, *Dromius angustus*) are missing from the Baltics (*Amara cursitans* and *A. majuscula*, although so far not found, can hardly be absent). The ability of the two groups to migrate is clearly illustrated by the fact that 9 of the flying species (= 60%) of the eastern group of Gotland are represented in Palmén's drift material (1944), but the western group is represented by only one specimen of *Amara majuscula* (and yet 9 of the 12 species of this group occur in Finland).

The eastern group in the carabid fauna of Gotland is clear proof of the important role played by the anemochorous (including anemohydrochorous) dispersal of winged insects from the east for the colonization of this island. It confirms the findings for Åland, Gotska Sandön and Fårön. Although Gotland lies considerably closer to the Swedish coast than to the Baltic coast (90 km as against 150 km). —The discovery of the two flightless species (*Demetrias monostigma*, *Trechus obtusus*) only in the eastern part of the island (at one locality each) is to be considered a coincidence, since both of them are missing from the Baltics and thus could not have immigrated from there, at least in the later period.

How careful one must be, in each case, in immediately deducing a late immigration from the east on the basis of restricted occurrence in eastern Gotland is shown by the discovery of the subfossil *Blethisa* from the Littorina period, especially along the west coast of the island (see p. 667). —On the other hand the somewhat larger distribution of lakes and swamps in eastern Gotland does not sufficiently explain the absence of hygrophilous species in the west.

The main question concerning the fauna of Gotland, the immigration of its especially striking species, which are more or less pronounced in the south, is treated below along with Öland and Bornholm (pp. 298 ff.).

293 **12. Öland**

This island is 137 km long and has a surface of 1,346 km^2, less than one-half that of Gotland. It is separated from the Swedish mainland by the Kalmarsund strait, which is only 3.4 km wide at the narrowest point (between Öld Stora-Rör and Små Skägganäs). The highest point (in Högsrum) is situated 55 m above sea level; the entire northern part (north of Bornholm) lies below the 14 m level.

Like Gotland, after being freed of inland ice Öland remained completely below sea level until the highest parts emerged almost simultaneously at the beginning of the Baltic ice sea period (Munthe, 1940, Plate II). Already before the end of the Yoldia period and until into the Ancylus period, thanks to the rapid emergence of the land, the southern part of the island had a larger size than now. The existence of any land corridor southward to the German

*Certainly also *Harpalus luteicornis*, although it was not possible to examine the eastern Baltic material with regard to *H. winkleri*.

Baltic Sea coast at that time is as uncertain as in the case of Gotland. At any rate, the existence of such a corridor at the beginning of the Ancylus period between central Öland and the mainland of Småland has been assumed (Munthe, l.c., Plate X; Sterner, 1938, p. 14). As a result of the rise in sea level ("Transgression") during the Littorina period the entire low northern part of the island was again submerged. Biologically speaking this part is very young. Apparently it was formed again as a continuous land mass only after the Littorina period (at an average rate of land emergence calculated at 25 cm per century by Witting, 1943, p. 28, this would have been about 4,000 years ago). The first plant immigrants belonged to the Arctic element (*Dryas, Salix "polaris"*; Hemmendorff, 1897, pp. 44, 47; Lundqvist, 1928, p. 29), but in very short time there also appeared species generally considered as markedly heat-requiring ("wärmefordernd") (see Erdtman, 1946, as well as p. 309).

Öland is a single low level limestone plateau, slightly lower toward the east, but in the west (except the northern part) sharply demarcated by a steep step, the so-called Landborg. In front of it is a belt of fertile lowland up to 3 km broad. The tableland, especially in the south, is occupied over large stretches by the *Alvar*[†], which is so very characteristic of Öland. It is an almost level surface where the more or less fissured rocky ground is bare or covered with a very thin layer of eroded soil. In summer the Alvar dries up and supports a very peculiar, steppelike flora. —In other parts, i.e. in the center of the island,
294 the plateau is covered by moraine, which is cultivated or is overgrown with groves and bushes. —There are no rivers but there are numerous small lakes especially on the Alvar, although they are quite seasonal and usually dry up in summer. —The seashores are predominantly gravelly-stony, and are often overgrown with grass to the waterline. Only in the extreme north (the parish of Böda) are there sand dunes.

Discoveries of Stone Age building sites on Öland are sparse (Munthe, 1940, p. 193), but the scattered implements found show that the island was probably colonized by man at the end of the Ancylus period (Lundqvist, 1928, p. 79). The present population is about 28,000. Traffic is (and possibly always was) entirely with the Swedish mainland, especially Kalmar.

The *flora* of Öland (Sterner, 1938) is very similar to that of Gotland and gives the impression of being still richer. The following 11 vascular species ("large species") occur exclusively in Sweden and Öland:

Artemisia laciniata	*H. oelandicum*
Bassia hirsuta	*Orobanche purpurea*
Helianthemum canum	*Plantago tenuiflora*
H. italicum	*Ranunculus illyricus*

[†](Plant community consisting typically of mosses and calciphilous herbaceous plants that grow on steppelike shallow alkaline soils overlying Scandinavian limestones; suppl. scient. edit.).

Ulmus laevis *Viola alba*
V. elatior.

The 16 species in common with Gotland are discussed below (p. 299).

There is no comprehensive account of the *coleopteran fauna* of Öland but Wahlgren (1915, 1917) has collectively described the entire fauna of the Alvar[†] regions. The coleopteran fauna, and the entire soil fauna, are treated rather perfunctorily. Yet Öland may represent coleopterologically the best explored province of Sweden. Its fauna is extremely rich and includes a long series of species (discussed on p. 303) apparently not found in the rest of Scandinavia. However, among the 221 carabid species found (Table 9) this is solely true for *Calosoma investigator*, which was recorded only due to the possibly accidental occurrence of a single specimen.

The qualitative composition of the carabid fauna of Öland is markedly "normal," i.e. there is practically no deviation from the regions of comparison dynamically (Tables 10, 12), ecologically (Table 14) or with respect to
295 hibernation types (Table 13). This correspondence is striking in not being due to any identity of species composition between Öland and the two regions of comparison. Only a greater preponderance of xerophilous species (Table 14) in the fauna of Öland is noteworthy.

As in the case of the fauna of Gotland (p. 291), it is not possible to distinguish recently arrived immigrants in the fauna of Öland. Nevertheless, it is striking that the two species of *Bembidion*, namely *quadrimaculatum* and *rupestre*, that are common all over the Swedish mainland, were only discovered on Öland in 1938 and 1939 respectively, and that the latter species is known only by one specimen (Böda). They are probably late immigrants. The conditions of life may not be lacking, since both show a wider distribution in Gotland.

A clear picture of how the fauna of Öland could have been enriched at least temporarily by accidental migration was provided by insect drift material, rich in specimens, and observations by Brinck (in litt.) on June 5, 1943, on the barren sandy shore of Byerum on the west coast of northern Öland. The following 20 species of carabids were represented:

* *Acupalpus dorsalis*, 1 specimen
* *A. flavicollis*, 3 specimens
* *A. meridianus*, 2 specimens
Amara communis, 1 specimen
A. nitida, 1 specimen
A. tibialis, 17 specimens
* *Bembidion doris*, 3 specimens
* *B. gilvipes*, 3 specimens, d
* *B. guttula*, 1 specimen, d
B. lampros, 25 specimens, d
B. quadrimaculatum, 8 specimens
Clivina fossor, 2 specimens
Dyschirius lüdersi, 3 specimens
Loricera pilicornis, 1 specimen

[†](Plant community consisting typically of mosses and calciphilous herbaceous plants that grow on steppelike shallow alkaline soils overlying Scandinavian limestones; suppl. scient. edit.).

Microlestes minutulus, 9 specimens
* *Notiophilus aquaticus*, 8 specimens, d
* *N. palustris*, 2 specimens, d
N. pusillus, 1 specimen
* *Pterostichus minor*, 1 specimen, d
* *Trechus rubens*, 1 specimen

The species with an asterisk (*) are those found in biotopes quite unusual for the species. Six species ("d") are dimorphic, but were represented *exclusively by the macropterous form.* Hence anemochorous (possibly anemo-hydrochorous) transport is involved. The numerous occurrence of *Bembidion quadrimaculatum* (and the occurrence of *Acupalpus flavicollis*, of which only 3 other specimens are recorded from Öland) indicates that the point of origin of these animals was not in Öland. All these 20 species are found within the Swedish "region of comparison" (12a) and it may thus be assumed that transport occurred from that direction.

296 **13. Bornholm**

The surface of this island, whose space is nearly rhombic, is 587 km^2, less than one-half that of Öland and only one-fifth that of Gotland. It is situated closest to Skåne, at about 40 km. Rügen lies about 90 km away, the coast of Pomerania (near Kolberg) is only slightly farther.

The highest point, Rytterkanaegten, almost exactly in the middle of the island, is 162 m above sea level. Hence, unlike all the other islands considered (with the exception of Hogland), Bornholm was never completely submerged during the postglacial period. On the contrary, it is now generally assumed by geologists that during the early postglacial period Bornholm was connected with the north German coast by a broad, uninterrupted land corridor (for instance, Sauramo, 1942, maps on pp. 228, 231), and according to Munthe (1940, maps, Plate XI) remained so into the Ancylus period. For this land connection, under present conditions, an elevation of only a little more than 20 m would be required (Hofsten, 1919, p. 51). It is strange that Spärck, in his *Danish Zoogeography* (1940), says nothing about the faunistic significance of this corridor.

Geologically (Trap, 1921, p. 520) in the larger northern part Bornholm consists of granite, in the south it is made of Cambro-Silurian slate, sandstone and limestone rock, and in the west Mesozoic deposits, including cretaceous deposits. The rock is mostly covered with a thin layer of moraine. The shores are frequently rocky but in the south there is also quicksand. Bodies of standing water are very small and sparse but there are many small rivers. About two-thirds of the region is cultivated and the rest consists predominantly of *Calluna* heaths and forests, mostly of *Pinus*, which is cultivated.

Man seems to have colonized Bornholm during the Ancylus period, perhaps when the corridor with North Germany existed (Munthe, 1940, Plate XI). The present population is about 45,000 and the landscape is greatly affected by culture. Traffic has always been mainly with the other Danish islands

(especially with Copenhagen), and to a lesser extent, especially in earlier times, with Germany (particularly Lübeck) and Sweden.

Concerning the *flora* of Bornholm, as far as I am aware there is only the old list of Bergstedt (1883), but a compilation can easily be undertaken following Rostrup (1943). There is a richness of species. Some comparisons of the flora with Öland–Gotland and Ösel–Dagö are drawn below (p. 299).

The *coleopteran fauna* has unfortunately not been studied as intensively
297 as that of Öland and Gotland, but is known to such an extent that, with 226 species, its coleopteran fauna now stands out as the richest among all the islands here considered. Hence detailed comparison with the faunas of the two above-mentioned islands is possible. A list has been provided by Jansson (1933); additions have been made by West (1940–41; 1947) and to a large extent a list can be easily extracted from the *Catalogus* (1939).

In Denmark 8 carabids are found exclusively on Bornholm:

Bembidion dentellum	*Brachynus crepitans*
(*B. octomaculatum*)	*Dromius angustus*
(*B. semipunctatum*)	*Harpalus rufus*
(*B. transparens*)	*Lebia cyanocephala.*

The three species in parantheses are undoubtedly accidental immigrants (see West, 1940–41). The other 5 species are found in Öland and (or) Gotland.

The carabid fauna of Bornholm actually includes numerous transmigrating ("transgredierende") species, which are found only on the seashore and therefore cannot be considered truly native to the island. According to the information given by West (1940–41; 1947), this applies to at least the following 17 species:

Acupalpus consputus	*Calosoma sycophanta*
Agonum dolens	*Chlaenius nitidulus*
A. lugens	*C. sulcicollis*
Badister striatulus	*C. tristis*
Bembidion humerale	*Harpalus griseus*
B. octomaculatum	*H. signaticornis*
B. semipunctatum	*Miscodera arctica*
B. tenellum	*Stenolophus skrimshiranus.*
B. transparens	

Strikingly, this list includes not only 3 of the species unknown in Denmark but also 8 of the 30 species occurring in Bornholm but not found in Öland or Gotland (see list on p. 307).

Evidently the direct flight from other regions of foreign species that cannot live on the island has played a greater role in Bornholm than in Öland and Gotland. If the experimental findings with regard to Åland (p. 256), on the fairly precisely derived concept of insect flight direction in the evening, are

298 applied to Bornholm, we find that the German Baltic Sea coast (primarily Pomerania) is favorably situated as the starting point for a migration west and north touching Bornholm.

Different figures for the *dynamics* of the fauna of Bornholm (Table 12) are fully explained by such transmigrating species, as also the somewhat greater deficit of functionally brachypterous species in comparison with those of Öland–Gotland. On the other hand, the fact that the proportion of "purely" brachypterous species (i.e. excluding the functionally dimorphic species) is much *higher* in Bornholm is due largely (or entirely) to less available material of dimorphic species from Bornholm. As soon as more material of these can be studied, the number of "functionally dimorphic species" in Bornholm will certainly increase.

Ecologically (Table 14) the fauna of Bornholm like that of Öland shows a slight preponderance of xerophilous species, but besides, particularly in contrast with Gotland, almost as high a preponderance of forest species.

With regard to the hibernation types (Table 13), there is a complete correspondence with the two islands mentioned above. The conditions are thus "normal."

Comparison between the Large Baltic Islands (Öland, Gotland, Bornholm, Ösel–Dagö)

These islands have been treated above very briefly. An analysis of the character and history of their fauna is possible only on the basis of direct comparison in as much detail as possible.

It is advisable to begin with the *flora* of these islands. We will take Öland and Gotland as our starting point. They are in every way the best-known of the four insular regions.

1. Of the 11 plant species of *Gotland* listed above (p. 290) that are absent from the rest of Sweden 2 species (*Arabis nemorensis*, *Tofieldia calyculata*) are found on Ösel–Dagö but none on Bornholm.

2. Of the 11 Swedish species that occur only on *Öland* (p. 294) only one (*Viola elatior*) is found on Ösel–Dagö and none in Bornholm.

3. The following 16 Swedish species ("large species") occur only on *Öland* and *Gotland* (Sterner, 1938, p. 38; 1946).

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	Adonis vernalis	Ös	*Braya supina*
Ös	*Anacamptis pyramidalis*		*Coronilla emerus*
Ös	*Anemone silvestris*		*Fumana vulgaris*
	Apera interrupta		*Galium rotundifolium*
Ös	*Artemisia rupestris*		*Globularia vulgaris*
	Aster linosyris		*Orobanche alba*

	Potentilla fruticosa		*Veronica praecox*
B	*Ulmus foliacea*	Ös	*Viola pumila.*

The 5 species marked "Ös" occur on Ösel–Dagö. Only *Ulmus foliacea* grows on Bornholm.

4. Sterner (1938) also provides a list of species "that occupy a wide area on Öland but are found only as great rarities on the Swedish mainland." After excluding the species missing in Gotland and the now subdivided *Euphrasia stricta*, and finally *Juncus alpinus*, which corresponds poorly to Sterner's definition, the list is as follows:

	Alisma lanceolatum		*Melica ciliata*
Ös	*Androsace septentrionalis*	Ös	*Ophrys muscifera*
B, Ös	*Bupleurum tenuissimum*	Ös	*Orchis militaris*
Ös	*Carex tomentosa*	B, Ös	*O. morio*
B	*Cerastium pumilum*	B, Ös	*O. ustulatus*
B, Ös	*Cornus sanguinea*		*Oxytropis compestris*
Ös	*Gypsophila fastigiata*	B	*Poa bulbosa*
B	*Holosteum umbellatum*		*Prunella grandiflora*
Ös	*Hutschinsia petraea*	B	*Scandix pecten-veneris*
B	*Inula britanica*	B, Ös	*Tetragonolobus siliquosus*
Ös	*Juncus fuscoater*	B	*Vicia tenuifolia.*

Putting together such species from the four lists above, which can be considered as typical representatives of the "flora of Öland–Gotland," we find that 20 of them occur on Ösel–Dagö but only 12 on Bornholm. I will not speculate from this as to the history of immigration of the flora of Öland–Gotland (concerning the great difference between the flora of Gotland and Ösel, see Kupffer, 1925, pp. 120–121). But I may be permitted to conclude *that Ösel–Dagö shows a greater ecological affinity with Öland–Gotland than with Bornholm.* The reason is undoubtedly that the more or less horizontally disposed Cambro-Silurian rock of Bornholm plays a minor part. On the other hand at many
300 places on Ösel-Dagö dry limestone rock areas have been formed with a thin layer of soil, which largely correspond to the Alvar of Öland–Gotland. The correspondence is not only chemical but also physical (thermic, hygric, etc.) (see the section on "limestone species," pp. 177 ff.).

To return to the coleopteran fauna. The simplest way to give a statistical account of the faunistic (or floristic) affinity between two regions is to express the data, on the common species for example, as a percentage. The figures for the four insular regions treated here are given in the following Table:

Table 23. Number and percentage of carabid species common to the large Baltic islands

	In common with			
	Ösel–Dagö	Gotland	Öland	Bornholm
Ösel–Dagö (131 species)	–	108 = 82.4%	116 = 88.6%	109 = 83.2%
Gotland (main island, 195 species)	108 = 55.4%	–	176 = 90.3%	168 = 86.2%
Öland (221 species)	116 = 52.5%	176 = 79.6%	–	189 = 85.5%
Bornholm (226 species)	109 = 48.2%	168 = 74.3%	189 = 83.6%	–

Percentage figures of this kind are quite useful so long as the faunas of the two regions compared have nearly the same number of species (for instance, Öland versus Bornholm). Otherwise the comparison, so to speak, must be looked at "from both sides" (for instance, Ösel–Dagö versus Bornholm). It might perhaps be permissible to construct "affinity figures" in a simple way by taking the mean values of the percentages of common species of the two areas compared. An attempt to use such figures for the insular regions considered here is given in the following map (Fig. 23).

The following general conclusions concerning the carabid fauna seem justified: The greatest faunistic affinity holds between Öland and Gotland, the least between Ösel–Dagö and Bornholm. Both results are according to nature. It is interesting that the affinity between Bornholm and Öland (and
301 also with Gotland) is so great that it opposes the floristic findings above. Besides, it is noteworthy that the affinity of Ösel–Dagö with Öland is even greater than with Gotland.

More useful than such conclusions based on purely numerical treatment of the entire fauna are comparisons that take into account the dynamic properties (the dispersal capability) of the species.

The functionally brachypterous carabid fauna of Öland and Gotland (main island) are easily seen from Tables 9 and 11 (pp. 206 ff.). Except for the constantly brachypterous species all of them are dimorphic with the exception of *Bembidion aeneum* and *Bradycellus harpalinus*. This makes a total of 70 species of which 68 are found in Öland and 59 in Gotland. No fewer than 57 species are common to both, a remarkable relationship which would give an "affinity figure" of 90.2 (cf. Fig. 23).

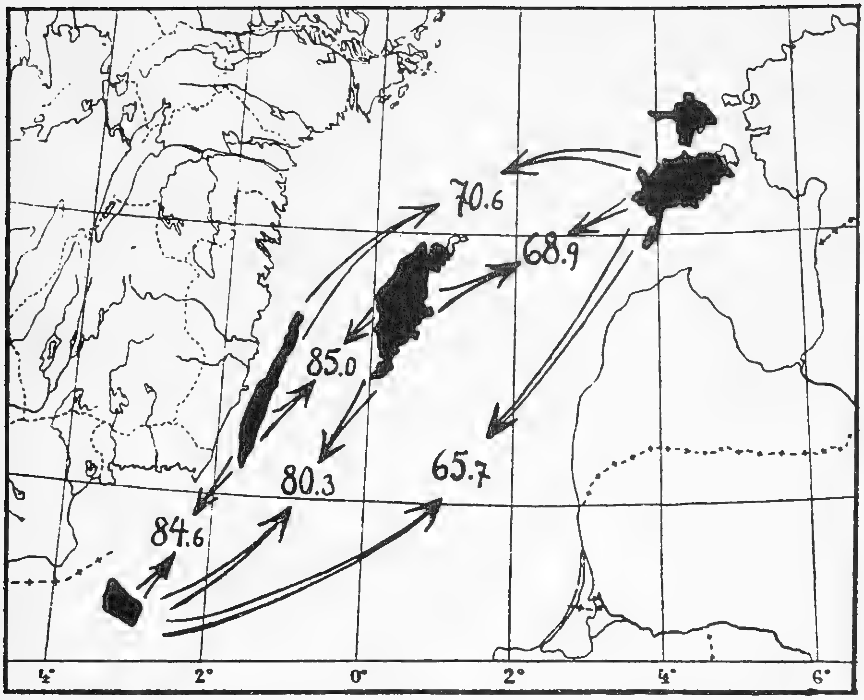


Fig. 23. "Affinity figures" of the carabid fauna from large Baltic Sea islands.

302 Comparison with Ösel–Dagö* and with Bornholm reveals the following:

Of the 68 functionally brachypterous carabid species of *Öland* 21 (31%) are missing on Ösel–Dagö and 7 (10%) on Bornholm.

Of the 59 functionally brachypterous carabid species of *Gotland* 20 (34%) are missing on Ösel–Dagö and 6 (10%) on Bornholm.

Of the 57 functionally brachypterous carabid species common to Öld-Gtl 18 (32%) are missing on Ösel–Dagö and 5 (9%) on Bornholm.

This great difference cannot be explained simply by insufficient exploration or by the poverty of the fauna of Ösel–Dagö. It is disproportionate to the number of species found on these islands and on Bornholm respectively (131 as against 226 species). In fact, contrary to the evidence from the flora, the difference shows *that the element of the fauna of Öland and Gotland that is difficult to disperse has a greater affinity toward the south than toward the east.*

*It could not be ascertained whether the dimorphic species occur in brachypterous form in Ösel–Dagö to the same extent as in Öld–Gtl. The figures were estimated taking into account the conditions on these islands. This qualification also holds for a few species in respect of Bornholm (see Table 11).

Hence this faunal element could not have immigrated across the sea from the east. From *where* it arrived may best be clarified by its most prominent species (geographically speaking)—those which in northern Europe or at least in Sweden occur exclusively in Öland and (or) Gotland. However, the carabids include only four such species, one of which (*Calosoma investigator*) is probably an accidental immigrant. We must therefore extend our research to *the entire coleopteran fauna* (Table 24).

Of these 60 species, as far as I know, only 6 (10%) are found in Ösel-Dagö (*Aphthona venustula*, *Chaetocnema mannerheimi*, *Coryssomerus capucinus*, *Drilus concolor*, *Harpalus punctatulus*, *Staphylinus pedator*), and only 5 (8%) on Bornholm (*Harpalus azureus*, *H. rupicola*, *Hylastinus obscurus*, *Ptomaphagus varicornis*, *Rhizobius litura*). This brings out the very characteristic nature of the coleopteran fauna of Öland and Gotland not only in comparison with the remaining Baltic islands, especially Bornholm, but also with the surrounding mainland regions.

Let us have a second look at this list of species restricted to Öland and (or) Gotland, this time from the viewpoint of the dynamics as we did earlier in the case of carabids.

Of the 60 species, 14 are *common* to Öland and Gotland. These include 5* (36%) *brachypterous and flightless* species (of *Drilus* only females; but *Harpalus azureus* has been found in Gtl in the macropterous form), none of which are even partially anthropophilous.

Of the remaining 46 species occurring on Öland or Gotland, *only 2 species are brachypterous* (4%), i.e. *Staphylinus winkleri*, restricted to Gotland, and *Lycoperdina bovistae*** found only on Öland. (The "Bornholm list" (p. 307) of 19 species also includes only one brachypterous species, *Acalles echinatus*, which also occurs on Gtl.)

Thus *the characteristic element of the coleopteran fauna common to Öland-Gotland, in contrast with the other Baltic islands* (with some exceptions) *and particularly with the surrounding continent, at the same time represents an element that is difficult to disperse, which must therefore be old.*

The details of this concept can now be examined in the context of the entire carabid fauna. Unfortunately Ösel–Dagö cannot be taken into consideration because the dynamic characters of the dimorphic species of these islands could not be judged.

**Drilus*, *Foucartia*, *Harpalus azureus*, *Staphylinus pedator*, and *Trachyphloeus alternans* are brachypterous (or dimorphic). Whereas *Galeruca oelandica* has much better-developed hind wings than *G. laticollis* (p. 243); and Jansson (1922, p. 71) has observed this species in large numbers, which could result only from swarming flight. *Ceuthorrhynchus schönherri* and *Hylastinus obscurus* turn out to be macropterous.

**The hind wings in 2 central European specimens of *Lycoperdina bovistae* are more reduced than in *L. succincta* (p. 246). The following "suspected" species have actually turned out to be macropterous: *Anthicus umbrinus*, *Apion armatum*, *A. millum*, *Ceuthorrhynchus molitor*, *Coryssomerus capucinus*; *Sitona cambricus* (according to Jackson, 1928).

303 **Table 24. Species of Swedish Coleoptera found only on Öland (Ö) and (or) Gotland (G; excluding small islands)***

Species common to both in bold face. The nomenclature is based on the *Catalogus* (1939).

Ö *Adelocera quercea* Hbst.
Ö *Agaricophagus cephalotes* Schm.
G *Aleochara spissicornis* Er.
Agrilus convexicollis **Rdtb.**
G *Anthicus umbrinus* Laf.
G *Aphthona venustula* Kutsch.
G *A. violacea* Koch.
Ö *Apion armatum* Gerst.
Ö *A. millum* Bach.
Ö *Atheta hybrida* Sh.
Ö *Attagenus punctatus* Scop.
G *Borboropora kraatzi* Fuss.
Ö *Bruchus luteicornis* Ill.
Ö *Calosoma investigator*
G *Cassida ferruginea* Gze
Ö *Ceuthorrhynchus molitor* Gyll.
C. schönherri **Bris.**
G *Chaetocnema mannerheimi* Gyll.
Ö *Colon rufescens* Kr.
G *Coryssomerus capucinus* Beck
Ö *Cryptocephalus elongatus* Germ.
Drilus concolor **Ahr.**
Ö *Elater nigerrimus* Lac.
Ö *Eremotes porcatus* Germ.
304 G *E. punctatulus* Boh.
G *Falagria thoracica* Curt.
Foucartia squamulata **Hbst.**
Galeruca oelandica **Boh.**
Harpalus azureus
H. punctatulus
Harpalus rupicola
Ö *Helophorus semifulgens* Rey.
G *Heterocerus intermedius* Ksw.
Hylastinus obscurus **Mrsh.**
Ö *Lycoperdina bovistae* Fbr.
G *Microglotta longicornis* Er.
Ö *Mordellistena brevicauda* Boh.
M. neuwaldeggiana **Panz.**
G *Nanophyes circumscriptus* Aubé.
Ö *Omophlus rufitarsis* Leske.
G *Onthophagus taurus* Schrb.
G *Ontophilus striatus* Forst.
Phyllotreta diademata **Fbr.**
G *Pilemostoma fastuosa* Schall.
Ö *Ptomaphagus varicornis* Rosh.
G *Rhagonycha femoralis* Brull.
Rhizobius litura **Fbr.**
Ö *Rhopalopus femoratus* L.
Ö *Scolytus pygmaeus* Fbr.
Ö *Sitona cambricus* Steph.
Ö *Smicronyx seriepilosus* Tourn.
Staphylinus pedator **Gr.**
S. winkleri **Bernh.**
G *Stenus neglectus* Gerh.
Ö *Teredus cylindricus* Ol.
G *Tomoglossa luteicornis* Er.
Trachyphloeus alternans **Gyll.**
G *Trox hispidus* Pont.
G *Urodon suturalis* Fbr.
Ö *Xyleborus monographus* Fbr.

It is worth studying the dynamic character of the carabids common to
305 Gotland, Öland and Bornholm in different combinations. This compilation can easily be made, using Tables 9, 11 and 12.

*Some doubtful species have been omitted (*Agrilus scaberrimus* Rtzb., *Anthonomus pyri* Koll., *Smicronyx jungermanniae* Reich.; also *Attagenus piceus* Ol and *Nausibius calvicornis* Kug., which have certainly been introduced anthropochorously). Additional information after the publication of the *Catalogus* (1939) was obtained from the literature and letters from Messrs. Anton Jansson, Nyholm, and Palm.

The following result is obtained:

Common to Gtl* and Öld:

192 species, of which 60 are functionally brachypterous = 31.3%

Common to Gtl* and Bornholm**:

176 species, of which 54 are functionally brachypterous = 30.7%

Common to Öld and Bornholm**:

189 species, of which 59 are functionally brachypterous = 31.2%

Common to all three areas* **:

169 species, of which 52 are functionally brachypterous = 30.8%.

All these figures of brachypterous species are as high as or higher than they are for the fauna of each individual island (namely Bornholm; Table 12). They show *especially that elements that disperse with difficulty are represented in the fauna common to Öland–Gotland and also Bornholm.*

A summary of the ideas so far considered might be appropriate at this stage:

1. The distribution of the flora shows a greater ecological (possibly also historical) affinity between Öland–Gotland and Ösel–Dagö than with Bornholm.

2. On the other hand the faunistic relations (at least with regard to carabids) are much more pronounced with Bornholm than with Ösel–Dagö. This affinity is especially pronounced in the case of flightless and soil-bound species and forms and may thus be due to the *history of immigration*.

3. The pronounced heat-requiring element in the coleopteran fauna of Öland–Gotland, quite peculiar for our latitudes, is poorly represented on Bornholm. It is significant that of these species those which occur both in Öld and in Gtl are largely flightless. The same in general holds for carabids common to the two islands and Bornholm.

This contradicts our observations (p. 271) while dealing with the fauna of the outer islands in the Gulf of Finland. We found that the functionally brachypterous species showed a lower constancy† on different islands than the flying species and forms. These constitute a *recent fauna that has immigrated across the sea*.

306 This brings us to the core of the problem. Can one *explain the richness and peculiarity of the fauna* (and flora) *of Öland–Gotland without the assumption of a postglacial land connection*? Lohmander (1946), the most recent author to deal with this problem although unfortunately in very condensed form, is inclined to affirm one. Great importance must be attached to his statement, for being a field zoologist he has more experience than any other researcher,

*Including Fårön and Karlsöarna.

***Agonum moestum* and *Bembidion assimile* are considered macropterous for Bornholm, whereas *B. gilvipes* is considered brachypterous (although no material was available) (cf. Table 11).

†(Ecological term; suppl. scient. edit.).

by all means with regard to the soil fauna of Öland and Gotland. (But also see Wahlgren, 1948, pp. 187 ff.)

No land connection can be "proved" by faunistic or floristic facts alone. Through them we can argue a greater or lesser *possibility* of such a connection; the verdict must be left to the geologists. My "believing" as to a direct post-glacial land corridor between Öland–Gotland and northern central Europe is based on the following reasons, the basis of which has largely been described above:

1. A very large number of species common to Öland-Gotland (79.6% of the carabid fauna in Öland, 90.3% of that in Gotland) is difficult to explain with identical environmental conditions alone, in view of the distance separating these islands. We would have to assume an almost unlimited dispersal capability for these species over a short period of time.

2. The hypothesis of immigration of the entire fauna of these two islands across the sea is contradicted by the high percentage of functionally brachypterous species (almost as high as that of the surrounding mainland; Table 12).

3. The most remarkable features are shown by the species of Coleoptera that are peculiar to Öland and (or) Gotland (missing from the rest of Sweden). Most of them are winged, but with some important exceptions: Of those 14 species common to the two islands, more than one-third (5 species) are flightless. Moreover the carabids common to Öland–Gotland reveal a higher percentage of brachypterous species than the fauna of each individual island. Anyone insisting on immigration across the sea must therefore assert that the passive transport of soil-bound animals is more effective than active flight. This would be absurd. On the contrary, these facts in my opinion indicated that Öland and Gotland possess a common nucleus of soil-bound species, which arrived through terrestrial immigration on a common route.

307 4. A comparison with the fauna of Bornholm. —Against the above list of species of Coleoptera of Öland and (or) Gotland missing from the rest of Sweden (p. 303), and of which only 5 species occur on Bornholm, it would be instructive to draw up another list of *Danish species found only on Bornholm* (Ö—Öland; G—Gotland):

B	*Acalles echinatus* Germ.	G	*Dromius angustus*
	Agathidium haemorrhoum Er.	ÖG	*Geodromicus plagiatus* Fbr.
ÖG	*Bembidion dentellum*	Ö	*Harpalus rufus*
	B. octomaculatum		*Hylurgus ligniperda* Fbr.
	B. semipunctatum	ÖG	*Lebia cyanocephala*
	B. transparens	ÖG	*Leptura maculicornis* De G.
ÖG	*Bidessus hamulatus* Gyll.		*Melanotus punctolineatus* Peler.
	Bledius tibialis Heer	ÖG	*Quedius nemoralis* Baudi
ÖG	*Brachynus crepitans*	ÖG	*Tachyta nana* Payk.
	Bruchus viciae Ol.		

Of these 19 species 9 occur on Öland, 10 on Gotland (moreover *Bambidion transparens* and *octomaculatum* on Fårön, *Bledius tibialis* in Gotska Sandön)! Eight species are missing from both islands, but these include 3 species of *Bembidion*, which are to be considered accidental immigrants on Bornholm (p. 297).

A similar result is obtained by a study of the dynamic character of Öland–Gotland species missing on Bornholm, and vice-versa:

Of the species of Gotland*:
  29** are not found on Bornholm, of which 8 are functionally brachypterous = 28%
Of the species of Öland:
  34** are not found on Bornholm, of which 9 are functionally brachypterous = 26%
Of the species of Gotland* and Öland:
  23** are not found on Bornholm, of which 7 are functionally brachypterous = 30%
Of the species of Bornholm:
  56 are not found in Gotland*, of which 11 are functionally brachypterous = 20%
Of the species of Bornholm:
  36 are not found in Öland, of which 3 are functionally brachypterous = 8%
Of the species of Bornholm:
  30 are not found in Gotland* and Öland, of which 2 are functionally brachypterous = 7%.

The following conclusion can be drawn: The fauna of Bornholm, in spite of the larger number of species, is much less peculiar than that of Öland and Gotland. Above all, the species characteristic of Bornholm are less soil-bound and without dispersal difficulty, the opposite of which was used as evidence for a land corridor in the past. This has indeed been generally assumed! The maps by Munthe (1940, Plates II, IV, X, XI) and Sauramo (1942, pp. 228, 231) show a land connection between Bornholm and the north German coast during the Yoldia period as well as the early Ancylus period (Munthe); v. Hofsten (1919,
308 pp. 54 ff.) lists a series of faunistic facts that support the assumption of a land connection. Are we not therefore justified in assuming a postglacial land connection for the immigration of the fauna of Öland and Gotland? With their greater richness both or relictlike isolated species and of soil-bound species that have difficulty dispersing these islands bear a still greater "continental" character than Bornholm.

As already mentioned (p. 289), Munthe originally believed that a direct

*Including Fårön and Karlsöarna.

**Taking into account *Agonum moestum* and *Bembidion assimile*, which have been found on Bornholm only in the macropterous form.

land connection with northern Germany and Öland–Gotland was probable, but later changed his mind, since in the maps in his recent contribution (1940) he shows only some isolated islands south of these two islands during the Yoldia periods and the early Ancylus period. Sauramo's maps (1942) show only a moderate displacement northward of the German Baltic Sea coast well into the Ancylus period. The hypothesis of the South Baltic land corridor is therefore no longer "modern." On the other hand it is naturally much more difficult to determine the outermost limit of a regression that now lies below sea level than that of a rise in sea level ("Transgression") that has left behind more or less distinct shorelines. With respect to the first of these, the maps both by Munthe and by Sauramo are purely hypothetical and the professional geologists whom I asked about this were very antagonistic with their opinion about the existence of a possible postglacial land connection in the South Baltic Sea region. From the geological viewpoint we can evidently expect to find definite evidence only if systematic core samples are taken from the bed deposits in the Baltic Sea. Since the technological prerequisites are now available we may hope such a study will not be long in coming.

While the geologists (especially Munthe, 1910) were more inclined to assume postglacial land connections with Öland and Gotland, the biogeographical consequences were diligently exploited by botanists and zoologists. Since the climate in the early Ancylus period, when according to Munthe the regression was at its greatest, was believed to have been too severe to permit the immigration of pronounced thermophilous species, much weight was attached to Munthe's assumption (1910, pp. 91–93) that Öland–Gotland were again connected with the South Baltic coast by a new land corridor during the transition to the Littorina period. Wahlgren (1917, pp. 88–96) thinks that the pronounced thermophilous species of the fauna and flora of Öland only immigrated during that second
309 period. V. Hofsten (1919, pp. 62–63) and Ekman (1922, pp. 379–380, pp. 429 ff.) are much more circumspect with regard to the existence of a second land connection. On the other hand Ekman (l.c., p. 429) thinks that the first land connection (until the beginning of the Ancylus period) could have played no role for "comparatively heat-requiring animals" (translated).

However, the problem has reached a somewhat different dimension as a result of pollen analysis in recent years. In the "late glacial" deposits (at any rate not younger than the oldest Ancylus period; cf. Lundqvist, 1928, p. 29) of Lundamosse (Öld Kastlösa), Erdtman (1946) found the pollen of *Artemisia* and *Helianthemum* as well as of *Oxytropis compestris*. Sterner (1946) suggests that the first of these may belong to *Artemisia rupestrix**. Iversen (1945) reports that *Helianthemum* pollen of the *oelandicum* type is common in the strata of the older

*However, in view of the increasingly common discoveries of subfossil *Artemisia* pollen, largely replacing the earlier "*Salix* pollen," in unexpected places, even in the interior of Lapland (Lyl Stensele, Langvattnet, 410 m above sea level; Erdtman, 1943), one is inclined to scepticism and to ask: Which species of *Artemisia* is involved here?

Dryas period throughout Denmark. It appears as if several of the plants typical of Öland–Gotland immigrated much earlier than we suppose. If the assumed land connection with Central Europe lasted into the Ancylus period it is highly probable that it was utilized by the plants and animals of present-day Öland–Gotland which we consider distinctly heat-requiring. Then there is no need of a second, later land connection even from the biogeographical viewpoint.

Relicts of the time of the first colonization of Gotland may include the plants *Pinguicula alpina* (also in Ösel) and *Bartschia alpina*. Their counterparts among the carabids are *Miscodera arctica*, *Nebria gyllenhali* and *Patrobus assimilis*. The last of these is constantly brachypterous. All three are missing on Öland, whose flora instead includes *Viscaria alpina* and *Poa alpina*.

A few words should be added on the land connection which, according to Munthe (1940, Plates X, XI), existed during the transition from the Yoldia to the Ancylus period, between Öland and the Swedish mainland (Småland). This has been taken as definitely established by Sterner, among others (1938, p. 14) (but it has not been accepted by Sauramo, 1942). Possibly it is to
310 this connection that Öland owes the functionally brachypterous species of its carabid fauna not found in Gotland (including the smaller islands) namely:

Amara infima	*Cymindis vaporariorum*
Carabus cancellatus	*Leistus rufescens*
C. coriaceus	*Metabletus foveatus.*

Yet at present *Amara* and *Carabus coriaceus* seem to be missing even from the adjacent Swedish mainland (region of comparison, 12a).

The occurrence of other striking species in the fauna of Gotland that do not exist in Öland can also be explained in this way. These are (after Ekman, 1922, p. 434; Noréhn, 1946; Nordström, 1946):

Arvicola terrestris	*Anguis fragilis*
Microtus agrestis	*Rana temporaria*
———	*Triton palustris*
Parus borealis	———
P. palustris	*Augiades sylvanus*
Picus viridis	*Pararge maera*
Tetrao urgallus	*Saturnia pavonia.*

However, the supposed land connection between Öland and Småland evidently cannot explain the immigration of the fauna of Gotland. On the contrary, it would not add to understand the striking correspondence between the fauna of Öland and Gotland. One may even urge the following viewpoint: *If a faunistically effective postglacial land connection existed between Öland and Småland the assumption of a direct terrestrial contact of Öland and Gotland with the South Baltic coast is all the more necessary.*

Finally two special cases:

1. The dimorphic species *Harpalus azureus* shows a peculiar distribution of macropterous and brachypterous individuals on Gotland (map in Fig. 34, p. 375). The species is found to occur in the north of the island only in macropterous form, with the exception of a single specimen found near Fårösund. Possible explanations are either that the species was displaced south by the decline in subatlantic temperatures and was later able to recolonize the
311 lost areas in northern Gotland only through the winged form; or that this displacement was brought about by the rise in sea level ("Transgression") in the Ancylus period (see map in Plate X in Munthe, 1940; the rise in sea level in the Littorina period was less extensive). If the latter assumption is correct, although unprovable on the basis of available material, then this heat-requiring species must have immigrated before the Ancylus maximum.

2. *Calathus mollis* (map in Fig. 28, p. 368). In my opinion the geographical distribution of the two forms of this dimorphic species permits rather bold conclusions about the immigration routes. First of all it is clear that no part of the Swedish stock could have come through the main Danish islands. From there (Copenhagen region) only one macropterous specimen has been found of the only subspecies *erythroderes* occurring in our region, whereas Jutland and Fyn constantly support the macropterous *forma typica*. Now Skåne had a direct land connection with the south during the early Ancylus period (but not later). We must assume that the immigration of the brachypterous form to Skåne took place at that time, and that Bornholm was colonized simultaneously. On the assumption of a later dispersal across the sea the absence of the brachypterous form from Sjaelland is inexplicable. *Carabus intricatus*, the most interesting flightless carabid of Bornholm, which is likewise missing from Sjaelland but occurs in southeastern Skåne, has apparently had the same history. Later, possibly after its subsequent isolation, Bornholm was also colonized by the flying *forma typica* of *Calathus mollis*; this happens to be the only region, at least north of Germany, where the two subspecies coexist.

At another place (p. 370), fairly detailed reasoning has been provided according to which the Öland–Gotland stock of *Calathus mollis* cannot represent an offshoot of the stock that immigrated through Skåne. That must be the result of a different immigration. What interests us here primarily is that the colonization of Bornholm and Skåne by the brachypterous form must be assigned to the early Ancylus period, *when the distribution of land and water in the southern Baltics with the most favorable for the assumed formation of a land connection with Öland–Gotland.* In my opinion *Calathus mollis* reached Öland and Gotland at this time by this route, coming from the south, along with numerous other species with difficulty of dispersing, and species generally considered highly heat-requiring, which, perhaps have to be admitted,
312 are more properly to be recognized as *continental* species, especially depen-

dent on warm, dry summers*. Already at the beginning of the Ancylus period the climate must have been very dry (see Nordhagen, 1933, p. 171), and the great expansion of land in the southern Baltic must have worked in the same direction. Gross (1931, p. 95) and Wagner (1940, p. 129) place the maximum temperature of the postglacial warm period already in the Ancylus period (also see pp. 663 ff.).

14. Ven

This small island of 7.5 km² situated in the Öresund strait lies 4.5 km off the Swedish coast (Skåne) and 8.5 km off the Danish coast (Sjaelland). It is a horizontal plateau of cretaceous formation covered with fertile glacial clay. It attains a level of about 40 m above sea level and drops sharply to the sea on all sides. The steep shores are made of loam or sand fringed by narrow, flat, gravelly or sandy shorelines. The slopes are very unstable as the soft material easily collapses, especially under the impact of a stormy sea.

Almost the whole island is arable and virtually without forest. There are no lakes or rivers thus a striking poverty of biotopes. The population exceeds 1,100. The traffic, always brisk, was once with Denmark, to which the island belonged until 1658, and since then predominantly with Sweden (Landskrona). Small ships can dock.

Shortly after the last glaciation Ven was part of the firm land connection between Jutland and southern Sweden through the Danish islands, and thereafter may not have been completely covered with water at any time. The rise in sea level ("Transgression") during the Littorina period was too slight in these southern parts to affect the perimeter of the island to any extent. Just at this time, at the beginning of the early Stone Age, Ven was colonized by man (G. Andersson, 1902a).

With respect to Coleoptera the exploration of the island has not been exhaustive. However, Palm (1935) provided an important account, especially
313 of the fauna of the shore slopes. Various other entomologists have made random collections. So although we do not know the actual number of species on the island we certainly know the approximate composition of the beetle fauna.

The carabid fauna shows a pronounced preponderance of dimorphic species but a deficit of brachypterous species (Table 10). On the basis of the functional dynamic groups there is a deficit of flightless forms, which is surpassed only by that of Gotska Sandön and the Finnish outer islands (Table 12).

Ecologically (Table 13) there is a poor representation of the forest element and a considerable deficit of the xerophilous element, probably because

*The severe winters of 1939–40, 1940–41, 1941–42, seem not to have caused any reduction of the xerothermic element of the fauna of Öland–Gotland, as I found from the collections made in Gotland in 1940, 1945, 1946, 1947 and in Öland in 1946 and 1947, particularly of the "limestone species" treated in the preceding section.

of the thorough cultivation of the island. The larval hibernators are poorly represented (Table 13).

The most peculiar trend in the fauna is undoubtedly the mentioned small number of flightless forms, since this is finally an island which undisputably had a postglacial land connection with the mainland.

There may be two reasons for this:

1. The great poverty of biotopes. First, forest species and inhabitants of fresh-water banks are absent. An estimated 15 functionally brachypterous species occurring on the mainland in Skåne must be missing from Ven for this reason alone or, in the case of dimorphic species, may be represented accidentally in the winged form (*Bembidion clarki*, *B. gilvipes*, *B. transparens*, *Pterostichus minor*, *P. vernalis*).

2. The complete cultivation of the island (see aerial photograph in Palm, 1935). This has primarily affected the species of the open terrain, for instance, many xerophilous species, estimated to be about 20 of the functionally brachypterous species occurring in Skåne. It is significant that in the genus *Carabus, C. nemoralis* alone, a species most favored by cultivation, has been found on Ven. Similarly, of the 8 remaining functionally brachypterous carabids occurring in Skåne that are more or less favored by culture only 2 (*Carabus cancellatus, Pristonychus terricola*) are missing from Ven, and the 4 dimorphic species of the remainder* (*Bembidion lampros, B. obtusum, B. ustulatum, Pterostichus vulgaris*) have also been found there in the brachypterous form.

314 Evidently, the culture has not only influenced the fauna of the island of Ven but has also introduced a number of species through passive dispersal. Among the other Fennoscandian islands considered here this might apply at the most to the islands in the Skärgård of Göteborg.

15. The Skärgård of Göteborg

Sufficient entomological exploration only occurred in Brännö, Styrsö and Donsö, belonging to the province of Vgl, and in Öckerö and Hönö, located farther north in the province of Boh. The characteristics of the two groups of islands are quite different and they would best be treated separately. But in the older collections of the entomologists of Göteborg (Sandin, I.B. Ericson, and others) animals only show the locality label "Skärgård of Göteborg," so it is impossible to allocate this material.

In the northern group above all *Öckerö* was studied. With a surface of 3.5 km^2, it is largely rocky and devoid of forest. The distance from the mainland is 3 km. The dominant plant is *Calluna*. The shores are rocky or gravelly. There are no lakes, but on the seaward side, close to the shore, there is a small peat bog. Chiefly because of the abundant occurrence of *Carabus clathratus*

*The two remaining (constantly brachypterous) species are *Calathus fuscipes* and *Patrobus atrorufus*.

and *Pterostichus aterrimus* this has been a favorite destination of Göteborg's collectors. —The island of Hönö, which has only occasionally been explored, is somewhat larger and is of identical nature.

In the southern group only *Styrsö* has been entomologically explored to some extent. With a surface of 4 km^2 it is mostly rocky as well. But because of the dense forests (mainly plantation) and largely well-cultivated valleys it looks like the mainland. The distance from the mainland is almost 5 km. It is a much-visited bathing and health resort. —Neighboring Brännö (area 3.2 km^2) and Donsö (area 1.6 km^2) are less wooded.

The two groups of islands have a total population of more than 8,000 and are thus relatively densely populated. The population, especially in the northern group, is engaged mostly in fishing and settlement is concentrated in fishing villages (Swedish: Fiskelägen). This specialization means having to import most of the necessities of life—wood, cereals, potatoes—from Göteborg, a city which receives the fishing products. Hence there are considerable pos-
315 sibilities of passive dispersal for insects, perhaps more than for any other Fennoscandian islands considered here.

These islands have never had any land connection during the postglacial period. However, at least those in the south had already emerged from the sea before the Ancylus period and were colonized during that period (Munthe, 1940, Plates II, X). For the diagram of a pollen from a small bog in Björkö, see Sandegren and Johansson (1931, p. 122).

Our knowledge of the carabid fauna, with 87 species, is certainly not complete but it may be possible to evaluate the qualitative composition at this stage. The striking absence of any forest element (Table 14) is not matched on any of the other islands. An estimate based on Table 9 shows that this element of the Fennoscandian insular fauna generally comprises more than one-half of the brachypterous or dimorphic species. It is all the more noticeable that these islands show an abundance of functionally brachypterous species (Table 12). However, it is symptomatic that the four dimorphic species of the Fennoscandian Region that apparently are favored by culture (*Bembidion lampros*, *B. obtusum*, *B. ustulatum*, *Pterostichus vulgaris*), have been recorded on the islands only in the flightless form (Table 11). There is no doubt that anthropochorous transport has played a major role in the colonization of these islands. I do not want to decide the conspicuous deficit of larval hibernators (Table 13) is to be explained by the indigenous (non-anthropochorous) element having immigrated chiefly in winter (with drift ice). However, it must not be forgotten that especially Brännö, being close to the estuary of the Göta-Älv river, holds all possibilities to receive all kinds of drift material (also with drift ice) transported down the river. Its position is similar to Hailuoto's (p. 235).

At any rate the element that has arrived independent of man is appreciable. Among others it includes such functionally brachypterous species as *Bembidion aeneum*, *Carabus clathratus*, *Cymindis vaporariorum*, and *Olistho-*

pus. As far as is known these are missing from the similarly situated Hvaler islands, and it should not be forgotten that the larger islands of the Skärgård of Göteborg are considerably older.

16. Orust

This island, with a surface of 336 km^2, is the largest island off the west
316 coast of Sweden. It is less isolated, with the mainland lying to the north and east, and the large island of Tjörn in the south. The separating straits are only 0.3, 0.2 and 0.1 km wide, respectively.

The landscape is variable, mostly rocky, but with many broad valleys with argillaceous soil. Most of them have been cultivated, but some still have deciduous or mixed forest, which is also found on any slopes that have not been cultivated. The shore is mostly rocky except for some loose deposits, rock, gravel, sand (but not sandy dunes) or loam. In the east, there are some fair-sized lakes which are entomologically almost unknown.

The highest point of the island, in the west, is 100 m above sea level. This signifies that the first parts emerged from the sea shortly before the beginning of the Ancylus period, at about the same time as the islands of the Skägård of Göteborg considered earlier. The first colonization may have taken place during the Ancylus period (Munthe, 1940, Plates II, X).

The present population of the island is about 19,000, engaged in fishing and cultivation. The island is almost self-sufficient with respect to foodstuffs, wood, etc. Despite the proximity of the mainland (the city of Uddevalla is only a little more than a mile away) the possibility of anthropochorous immigration of insects is much less than in the case of the Skärgård of Göteborg. There is of course car traffic with the mainland by ferry.

Our knowledge of the 87 known species of carabids derives from the numerous random collecting by various entomologists. It bears no relation to the actual number of species, which may be about 50% higher. Ecologically (Table 14) the fauna shows a very high deficit in xerophilous species, which is understandable given the very sparse occurrence of sandy soil; the forest component is normal. The preponderance of brachypterous species (Tables 10, 12) is almost the same as on the islands of the Skärgård of Göteborg. However, for the reasons given above it may not be possible to explain this fact as the consequence of anthropochorous transport. "Natural" passive dispersal, even of the brachypterous element, is possible to a great extent, due to the very narrow surrounding straits. The pronounced preponderance of larval hibernators (Table 13) might show that this immigration can also take place in summer, i.e. the salt water does not obstruct hydrochorous transport over such short stretches.

317 **17. Hvaler**

Only the main island, Kirkeöy, has been studied entomologically. With a

surface of 26 km^2 it lies about 4 km from the nearest mainland northward and eastward (Sweden). Some of the smaller islands of the Hvaler group are still closer.

The highest point is only 74 m above sea level, so the island emerged comparatively late, in the early Littorina period. It attained an appreciable size only after the first great rise in sea level in the "Tapes" period (Nordhagen, 1933, p. 134; Munthe, 1940, p. 137, Plate XIII; Sauramo, 1942, p. 241).

Kirkeöy (Collett, 1866) largely consists of rock (granite), bare or overgrown with sparse coniferous forest. The deciduous forest (including *Tilia* and *Corylus*) is only of small extension. The shores are largely sandy, covered with *Carex arenaria, Cakile* and the like. Of particular interest is the markedly eutrophic lake Arekilen, formed when a sea bay was cut off. Its swampy shore has a very rich vegetation, chiefly consisting of *Phragmites*, but also of *Typha latifolia*, *Rhyncospora alba*, *Acorus*, *Naumburgia*, *Dryopteris thelypteris*, *Utricularia* and the like.

The population, about 3,000 on all the islands, mainly lives off fishing, and the cultivated region is not large (Kiaer, 1885, pp. 201 ff.). There is brisk traffic with Fredrikstad and Halden.

The island of Kirkeöy has been fairly well explored by various Norwegian coleopterists (chiefly Collett, Munster, Natvig), and it may not be possible to add much to the 107 species known at present. Two species which the Norwegian scientists have found on this island, *Badister dilatatus* and *Odacantha melanura*, rate special interest. Both occur around Lake Arekilen (see above). Ecologically they are closely related, since both inhabit the vegetation-rich shores of eutrophic waters. They represent a small group of species with the same mode of life, found in Norway more or less sporadically only in the southeastern parts, which apparently immigrated from the region of the central Swedish lakes, i.e. from the east. Other examples of this group are *Chalaenius tristis* (also in Hvaler), *Oodes helopioides* and *Panagaeus crux-major*. As far as I am aware none of these species occur in northern Jutland (see maps in Part II).

Ecologically the carabid fauna shows a preponderance of xerophilous
318 species but still a more pronounced deficit of forest species (Table 14). A preponderance of functionally brachypterous species, as on the islands of the Skärgård of Göteborg and on Orust, is not found here (Table 12). The conditions are normal as compared to the region of comparison. As in Orust, the larval hibernators show plus values (Table 13), which indicates a predominantly summer immigration of the flightless element. It is possible that, situated some 10 km away, the estuary of the Glomma (the biggest river in Scandinavia) favors hydrochorous transport not only because of its active current, which might transport pieces of wood, reeds, etc. (including those on or

in icefloes) down to Hvaler, at least during spate in spring*, but also due to the reduction in the saline content of the sea (Collett, 1866, p. 2). This is a decisive factor for the ability of insects to endure a hydrochorous transport of longer duration (see Palmén, 1944, pp. 154 ff.).

18. Hitra and Neighboring Islands

These islands are located off the outlet of the Trondheim Fjord. In addition to the big main island of Hitra (surface 634 km²), in the southwest there in Smöla (surface 214 km²), 8.5 km away, in the north Fröya (surface 147 km²) 6 km away, and finally the small island of Dolmöy (surface 15 km²), situated in the strait between Hitra and Fröya, close to Hitra. The island closest to the mainland is Hitra, separated by a long strait, which is only 4 km wide at the narrowest point.

Only Hitra has been investigated entomologically, unfortunately not at all thoroughly. On the other three islands respectively only 5, 5 and 3 (Smöla) carabid species have been recorded. These include 6 species so far not known from Hitra, but probably occur there, thus they have been considered.

Hitra (Helland, 1898) is predominantly mountainous (with granite, gneiss, greenstone, etc.), the highest point (Mörkdalstua) being 369 m above sea level. The low-lying areas are occupied chiefly by bogs and many small lakes; there are many streams. The forest area was once much larger; now continuous coniferous forest occurs only in discrete, restricted areas. Among the deciduous forest trees *Betula* dominates.

319 The population, comprising at least 4,000, depends on fishing and lives along the coast, where only small areas are cultivated.

The traffic is chiefly with Trondheim.

The other three islands (Helland, 1898, 1911) are markedly flat (the highest points range from 67 to 78 m above sea level) and boggy. There is no coniferous forest and even the deciduous trees (chiefly *Betula*) form shrubby forest only at some points.

The total number of 49 species of carabids known from these islands (43 of them from Hitra) would undoubtedly be augmented by 20% or more with thorough exploration. However, the composition already shows that the fauna represents perhaps the most interesting of all the Fennoscandian islands treated here.

The number of *functionally brachypterous species* in the Hitra Islands is *greater than on any other island* (Tables 10, 12), not only in aggregate but also vis-a-vis the region of comparison (18a). This despite the fact that these regions of comparison on the west coast of Norway (18a, 19a) actually show a high ratio of brachypterous species (Table 12). The *constantly* brachypterous

*Perhaps the unexpected finding of *Pelophila borealis* in Hvaler is to be explained in this way (Lindroth, 1935a, p. 584). But the insect is capable of flight.

species (Table 10) are more numerous (16.5%) particularly in the area 18a of comparison than in any other, and indeed the preponderance of these on the Hitra islands is particularly large (18.2%).

How is this to be explained?

1. One explanation would be that in these regions the dispersal of flightless species and forms would be especially favored, or (and) that selection eliminates the flying forms. Either case must be consequence of exposure to strong winds.

Fortunately, certain islands are counterparts, in being similarly exposed to the sea, including Dönna, Lökta, etc. (see below), and particularly the Frisian islands, Helgoland and the Scilly islands. The analysis of the fauna of the last-mentioned islands given below (p. 326) shows that none of them has such a high percentage of brachypterous species. With respect to the dynamics of their faunas, all are of quite normal composition, with the number of functionally brachypterous species ranging from 30 to 37% (maximum). When the Hitra islands are considered in this light, it appears that the dominance of brachypterous species could not originate from selection due to exposure to wind, at any rate not *at present time.*

2. There is still less to be said for explaining the peculiar composition of
320 the fauna of these islands with respect to passive dispersal by man. How small the effect of this agent has been becomes evident from the following:

In the Trondheim region (region 18a of comparison), 6 brachypterous or dimorphic carabids are found that are more or less clearly favored by culture: *Bembidion lampros, B. ustulatum, Calathus fuscipes, Carabus nemoralis, Patrobus atrorufus, Pristonychus terricola.* Of these so far only *Calathus* and *Carabus* have been found on the islands considered, the latter not on Hitra but only on Smöla.

The exceptional number of functionally brachypterous carabids in the Hitra islands, which even exceeds that of the Atlantic islands Lundy, Shetlands, Faeröer and Iceland (see below), lying outside our region *cannot have resulted from a postglacial immigration of the fauna from the Norwegian mainland.* The present fauna must be the direct descendants of the fauna of an ice-free refuge during the last glaciation (Würm), indifferent whether this included the present Hitra islands or whether it was situated farther out, due to a lower level of the sea (north of these islands is the shallow sea of Froan).

In this connection *Aëpus marinus* and *Trechus fulvus* deserve special attention. Their occurrence on Hitra marks the northernmost limit not only in Fennoscandia but in their total area, and this locality is markedly isolated, especially with respect to the species of *Trechus.* The seaward parts of western Norway have indeed been little explored, but the big gap of *Trechus fulvus* is occupied by the faunistically quite well-known region of Bergen thus the isolation of Hitra might actually be a fact. Both species are flightless and in my opinion true *relicts,* which is discussed below (p. 791) in detail.

The preceding discussion must not be taken to indicate that the fauna of the Hitra islands in its entirety represents an old "Würm fauna." It includes some species that are undoubtedly in part late postglacial immigrants. In this respect the case of the dimorphic species *Pterostichus minor* (see p. 387) is especially clear, it has reached the Trondheim region from the east (from Sweden). *Bembidion quadrimaculatum* is also an indubitable eastern migrant. —Moreover the most peculiar record, situated totally isolated, is that of *Dromius quadrinotatus* on Hitra. This species is associated with *Pinus*, and it is natural to assume introduction of the species along with conifers.

321 Finally we might allude to the fact that the fauna of the Hitra islands has no deficit of forest species (Table 14), which indeed might have been expected. However, it is only an expression of a situation found, for instance, on Iceland (Lindroth, 1931, p. 387), that animals which normally are more or less linked to forests, in a markedly oceanic climate (i.e. high humidity of the air and less sunlight), leave their exclusive mode of life and become more or less eurytopic (typical example: *Notiophilus biguttatus*. —For the same reason the strong deficit of xerophilous species is easily understandable.

19. Donnä and Neighboring Islands (Alstenöy, Heröy, Lökta)

This small group of islands, immediately south of the Arctic Circle, was selected because it was the only insular region off this part of the Norwegian coast that has been to some extent explored. It lacks a pronounced insular character because of the very narrow straits between the largest islands and the mainland.

Alstenöy has a surface of about 128 km^2; Dönna, north of it, is equally large (135 km^2); whereas the two remaining islands, Lökta in the north (area 17 km^2) and Heröy in the west (surface 6 km^2), are very small. The landscape is markedly barren and mountainous; the highest point (on Alstenöy) is about 1,066 m above sea level (Helland, 1907).

The rocks are composed of granite as well as slate and primitive limestone. Small lakes and running water are found on the large islands, otherwise the plain lowland is mainly swampy. The forests consist chiefly of sparse, low deciduous trees. They are somewhat better developed on Alstenöy, where there is also some sparse *Pinus* which hardly forms a forest stand.

The population, comprising about 3,000 persons, lives chiefly on fishing and commerce; the cultivated regions are small. Sandnessjöen (on Alstenöy) has active shipping connections, also with distant places.

The *carabid fauna* has not been systematically investigated. Nevertheless, the known 46 species may be closer to the actual number of species than, for instance, those known from the Hitra islands. As in the latter there is a marked deficit of xerophilous species, but there is a still greater one of forest species (Table 14). The preponderance of functionally brachypterous species is pronounced (9.2%) but it is not even one-half the number in the Hitra

islands. Hence we are not justified in taking the preponderance of brachypter-
322 ous species as evidence for a nearby situated Würm refuge. On the other hand it needs to be mentioned that among the flightless species of these islands there is only one, *Patrobus atrorufus*, that might be considered to some extent favored by culture. Despite brisk trade connections of these islands (particularly of the trading center Sandnessjöen) it would evidently be a mistake to attribute the composition of their fauna to passive dispersal by man.

20. Lofoten (and Vesterålen)

Strictly speaking Lofoten comprises only the westernmost islands, eastward to Austvågöy, but for our purpose all the islands west of Ofoten and Senja have been included, even Vesterålen. These together form Province 31 (see map in Part I) and to some extent represent a natural geographical entity. The northernmost of these islands is Andöya. The total land surface is about 4,650 km².

This is a great wall of rock more than 250 km long, which exceeds 1,000 m above sea level at several points (the highest peak, 1,286 m, is on Hinnöya) and is divided into islands separated by narrow straits. The closest distance to the mainland, only about one km, is on Hinnöya, the largest of the islands.

With the exception of the Lödingen region on Hinnöya, where there is also some *Pinus*, the islands are very poorly wooded (Helland, 1907, pp. 677 ff.) with *birch*, which usually forms sparse stands warped by the wind. On Vaeröy and Röst even birch is missing. —There are numerous but small bodies of water and streams.

The population (about 50,000) lives almost exclusively on fishing and a tiny region is cultivated. Most foodstuffs, chiefly cereals, must be imported. The frequent import of wood for building favors the passive dispersal of insects and plants. On the other hand the arrival of tens of thousands of fishermen in the peak season of cod fishing has only a small role, since the falls in the winter.

Entomologically, the Lofoten region has not been systematically explored but it has been visited by so many collectors at such widely separated points (see Strand, 1946a) that the number of carabid species now known (64 species) may be considered fairly definitive.

323 Let us first study this fauna in its entirety, as in Tables 9–14. As expected, the ecological grouping shows a deficit of forest species, but instead there is a slight preponderance of xerophiles (due to the absence of *Bembidion dauricum* and *Carabus problematicus* in the area of comparison, and so of little consequence). The division based on dynamics (Tables 10, 12) shows that the Lofoten region has the *greatest preponderance of functionally brachypterous species after the Hitra islands.*

However, in a region so much divided into numerous islands it is advisable in this respect to compare some of these among themselves, such as the three best-studied islands: Hinnöy, Hadselöy, Austvågöy—and in addition Vaeröy and Röst at the outermost tip of Lofoten, despite inadequate exploration:

	Distance from nearest mainland	Macropterous carabids	Functionally brachypterous carabids	Total
Hinnöy	<1 km	29 = 66%	15 = 34%	44 species
Hadselöy*	45 km	21 = 60%	14 = 40%	35 "
Austvågöy	33 km	22 = 54%	19 = 46%	41 "
Vaeröy and Röst	80 km	3 = 27%	8 = 73%	11 "
Lofoten as a whole	—	39 = 61%	25 = 39%	64 "

*It may be noted that Hadselöy is surrounded on three sides by larger islands, whereas Austvågöy is close to only one, to the east.

The farther an island is from the mainland or from larger islands, the greater the component of flightless forms in the fauna. In the Baltic Sea we found the opposite situation (for example, Gotska Sandön, outer islands in the Gulf of Finland). However, in the present case the reason is clear. It is *not* due to postglacial selection of the flying element on the outermost islands (cf. Hitra above, and the Frisian Islands on p. 326). Selection has presumably taken place, but during a much longer time, in a remote, harsh epoch, the Würm period. The refuges of that time were on or near the present-day outermost islands, and the postglacial invasion from the mainland, which naturally consisted predominantly (in these regions perhaps exclusively) of flying insects, barely reached these distant islands.

324 **21. Various Islands in Troms and Finnmark**

Toward the north the fauna gradually becomes poorer in species. On none of the small islands or groups of islands north of the Lofotens are so many species known that classification and calculation of percentages according to the Tables (10, 12–14) seem justified. An exception would be Tromsö, but it has a less insular character, thus cannot serve as a representative of the Nordic islands, some of which are very isolated.

I have therefore undertaken a simple division of the fauna of the five best-known islands north of the Lofotens (see map in Fig. 18) into dynamic groups, as I did above in comparing islands in the Lofoten region. Hence the use of a "region of comparison" has been dispensed with. —Sparre Schneider has provided excellent descriptions of the landscape and fauna of four of the islands concerned: Tromsö (1879, 1889), Hillesöy (1888, 1910), Nordfuglöy (1885), Kvalöy (1899).

A complete list of species is not given, since the records can be easily found in the sizable contribution by Strand (1946a).

The selected islands show the following figures:

Troms	Distance from nearest mainland	Macropterous carabids	Functionally brachypterous carabids	Total
I Tromsö	<1 km	26 = 63%	15 = 37%	41 species
II Hillesöy	20 km	9 = 56%	7 = 44%	16 "
III Nordfuglöy	27 km	8 = 44%	10 = 56%	18 "
Finnmark				
IV Kvalöy	< 1 km	17 = 59%	12 = 41%	29 "
V Mageröy	2 km	11 = 58%	8 = 42%	19 "

Compared with the mainland, all these islands have a preponderance of functionally brachypterous species. In the region of comparison for the Lofotens (20a) these constitute 28% of the fauna (Table 12). The similarly formed region of comparison for Mageröy (marked "21a" on the map, Fig. 18) includes 31% brachypterous species. The least preponderance is found on Tromsö, located in the inner part of the Skärgård and surrounded on all sides by mainland or larger islands. The maximum preponderance among the outermost skerries is found on Nordfuglöy. The principle and the cause are undoubtedly the same as in the Lofoten region.

It is interesting that Nordfuglöy, whose isolated, inaccessible position is
325 vividly described by Sparre Schneider (1885), has the highest preponderance of flightless species. For here is a test case, that this faunal element *cannot* have arrived by synanthropous transport.

Comparison with Some Islands Situated Outside the Region

Before summarizing the results of our studies on the Fennoscandian islands it is advisable to check the above concepts against other western European islands whose fauna is fairly well known. These are the following:

Helgoland (Dietze, 1939; Caspers, 1942; *Bembidion harpaloides* according to Netolitzky, 1916).

Sylt among the North Frisian islands (Stock, 1914; Zimmermann, 1935; *Olisthopus glabricollis* Germ. and *Pterostichus interstinctus* Sturm excluded, following Horion, 1941).

East Frisian islands. Among these only islands having more than 70 carabids were considered. These are the following:

Norderney (Verhoeff, 1891a; O. Schneider, 1898). —*Memmert* (Füge, 1919; Alfken, 1924; the species omitted were *Elaphrus aureus*, see Horion, 1941, and *Bembidion lunulatum*, presumably = *aeneum*) —*Borkum* (O. Schneider, 1898; *Harpalus "picipennis"* presumably = *vernalis*). —Of the islands omitted *Juist*, which is fairly well explored, has 63 known species (Alfken, 1891; O. Schneider, 1898).

West Frisian islands. Texel (Kempers, 1897). —*Terschelling* (Mac Gillavry, 1914; Reclaire, 1926) and *Vlieland* (Reclaire, 1930), with 52 and 48 known

species respectively, have been omitted.

Scilly Islands and *Lundy* off the southwest coast of England (Blair, 1931).

Isle of Man (Bailey and Britten, 1943, 1946).

The *Shetlands* and *Faeröer* (West, 1930).

Iceland (Lindroth, 1931).

Where appropriate the following were used as "regions of comparison": Hamburg region (Stern, 1926; Franck, 1928; Horion, 1941) for the North Sea islands; Northern Devon (Blair, 1931) for Scilly and Lundy. There is no suitable area of comparison for the three North Atlantic islands.

326 Division of the carabid fauna of the above-mentioned islands in dynamic groups is quite difficult. Above all it was not possible to obtain material of the *dimorphic* species for study in order to determine the form occurring on the island concerned, or possibly the occurrence *of both* forms. The dimorphic species have therefore generally been placed in a separate group, and the figures given below are best compared with those of Table 10 (p. 218).

With reference to the following survey (Table 25), it has to be mentioned as well, that of the species from the respective islands that do not occur in Fennoscandia only the following have been considered constantly brachypterous: *Abax parallelus* Dft., *Aepopsis robini* Lab., and *Bradycellus distinctus* Dej. (based on 3 specimens from Algeria; Kult, *in litt.*). The dimorphic species are *Cillenus lateralis* Sam. (Ganglbauer, 1892, p. 177) and *Pogonus chalceus* (Kult
327 and Makólski, *in litt.*). *Calathus piceus*, *Carabus granulatus*, *Demetrias monostigma* (although apparently constantly brachypterous, at least on Helgoland; Dietze, 1939, p. 309) and *Pterostichus niger* are dimorphic in Central Europe (p. 337) and are listed as such. However in western Europe, *Calathus mollis* seems to be constantly macropterous (Verhoeff, 1891b; see also p. 368)*. —The *Pristonychus* species and *Sphodrus* were ignored, being anthropobiont.

The occurrence of the flightless element (or more correctly the one that comprises the flightless species) is astonishingly regular, so that the islands in Table 25 are divisible into two well-defined groups. In the case of the three last-mentioned islands (Shetlands, Faeröer, Iceland) and moreover Lundy, this element constitutes almost one-half of the fauna and in the case of the other islands only about one-third. An intermediate position is occupied by the Isle of Man. It is striking that the divide passes between the neighboring island groups Scilly and Lundy. Both have the same "hinterland" (Cornwall) and are located within the part of the British Isles that was ice-free throughout the last glaciation, but their history has apparently been different. The figure of 36% functionally brachypterous species (maximum) of the Scilly islands must be considered "normal," since the "region of comparison" at the north coast of Devon (Blair, 1931) has 35%. Lundy (with 46%) thus occupies about the

*According to L. Benick *(in litt.)*, 17 specimens of *Calathus mollis* from Helgoland were all macropterous.

326 **Table 25. Carabids of some Western European islands divided into dynamic groups**

m=constantly macropterous; d=dimorphic (whether also on this island is unknown); b=constantly brachypterous

	m			d			b			b+d	Total
	species		%	species		%	species		%	%	number of species
Helgoland	25	=	68	10	=	27	2	=	5	32	37
Sylt	64	=	66	27	=	28	6	=	6	34	97
Norderney	48	=	63	23	=	30	5	=	7	37	76
Memmert	61	=	70	21	=	24	5	=	6	30	87
Borkum	67	=	68	23	=	23	9	=	9	32	99
Texel	50	=	63	21	=	26	9	=	11	37	80
Scilly	44	=	64	15	=	22	10	=	14	36	69
Lundy	30	=	54	16	=	28	10	=	18	46	56
Isle of Man	71	=	60	25	=	21	22	=	19	40	118
Shetlands	24	=	53	12	=	27	9	=	20	47	45
Färöer	14	=	54	6	=	23	6	=	23	46	26
Island	9	=	53	5	=	29	3	=	18	47	17

same position as Hitra vis-a-vis the Norwegian mainland.

The probable explanation for these faunistic differences among the three above-mentioned British insular regions is that only Lundy had an undisturbed faunal development since the last interglacial period. As already mentioned, this island was located beyond the edge of the Würm ice (Charlesworth, 1929, p. 336). It is so high (mean level about 120 m) that it can hardly have been affected by the postglacial rises in sea level ("Meerestransgressionen"). The Scilly islands probably were affected, their highest point lying barely 50 m above sea level, and they had hardly any postglacial land connection with the mother island (they are beyond the 30-fathom line). The Isle of Man was certainly glaciated during the Würm period, but probably had a postglacial land connection with the main island (Charlesworth, 1930, p. 383; Beirne, 1947, p. 346; this island lies within the 20-fathom line).

When comparing the "dynamic figures" for the Fennoscandian islands (obtained by adding columns d, (d), and b of Table 10), only in the Hitra islands
328 and among the peripheral skerries of the Lofotens and of Troms (p. 323) do we find figures for the inconsistently macropterous element as high or higher as in Lundy, the Shetlands, Färöer, and Iceland. And the cause must be the same: The major part of the fauna of these islands has survived the last glaciation *in situ* (or in the immediate vicinity). This allegation is especially motivated with regard to Iceland and the Färöer (Lindroth, 1931, p. 565), and we have now found identical conditions for islands which are situated close to the European mainland.

The "b+d element" on the first 7 islands in Table 25 (Helgoland to Scilly),

accounts for 34.0% as mean figure, thus corresponds fairly exactly to the mean figure 32.9% of the same element on the first 17 islands in Table 10 (until Hvaler). In all these cases postglacial colonization of the islands must have taken place. The North Sea islands (including Scilly) were of course all located outside the limits of the Würm ice, but have been heavily rearranged by wind and water (Schütte, 1927), and the northernmost of them might also have been adversely affected by the eustatic rise in sea level ("Transgression") in the Littorina-Tapes period.

Some of the Frisian islands are very young. *Memmert*, whose origin and development have been thoroughly studied by naturalists is said to have become colonizable for terrestrial plants and animals only around 1880 (Leege, 1913). Correspondingly, this island shows the lowest figure (30%) for the "b+d element" (Table 25)*. In Fennoscandia lower figures are shown only by Gotska Sandön (22.3%), the Finnish outer islands (26.0%) and, thanks to the numerous accidental immigrants (see p. 297), by Bornholm with 28.8%. The youthfulness of Memmert is compensated by its proximity to the larger islands Borkum and Juist, as well as to the mainland. —The converse applies to *Helgoland*, which has never been flooded by the sea in the postglacial period (Pratje, 1923, pp. 56–57). The pronounced dominance of macropterous species on this island is indeed strange, since it is believed to have had a land connection with the German mainland at least into the Yoldia period (l.c., p. 59). It is also interesting that the above-mentioned deficit was not compensated by anthropochorous transport.

An analysis of the *hibernation types* (as in Table 13) in the flightless component of the fauna of the islands considered here, may perhaps help to answer the question how these islands acquired this element. However,
329 specific division according to dynamic groups, as in Table 13, is not possible. Among the species not found in Fennoscandia *Abax parallelus* (Makólski, *in litt.*) and *Aëpopsis robini* (Burmeister, 1933, p. 99) have been considered as larval hibernators; *Cillenus lateralis* (ibid, p. 82), and with reservations *Bradycellus distinctus* and *Pogonus chalceus* (see data in Rapp, 1933, p. 60), as imago hibernators.

Table 26 shows the westward increasing component of larval hibernators in Europe (already noted by Larsson, 1939, pp. 510 ff.), which is shown especially by the high index numbers for the Shetlands, Färöer and Iceland and by the high index figures for Fennoscandia in Table 13 (Lundy is an exception, difficult to understand).

The North Sea islands are of special interest. All, with the exception of Helgoland, show low figures. This becomes especially evident if we select

*The very incompletely explored and equally young island *Mellum* (Schubart, 1920) has only 2 brachypterous and 3 dimorphic species out of the 21 carabid species found, i.e. altogether 24% of the fauna.

Table 26. Hibernation types of inconstantly macropterous carabids of some western European Islands (cf. Table 13, p. 230)

	A. Larval hibernators O+L+L	B. Imago hibernators I+I	Index A:B	Deviation of index from area of comparison*
Helgoland	6	6	1.0	+0.31
Sylt	10	23	0.43	−0.26
Norderney	10	18	0.56	−0.13
Memmert	6	20	0.30	−0.39
Borkum	10	22	0.45	−0.24
Texel	9	21	0.43	−0.26
Scilly	12	13	0.92	+0.13
Lundy	9	17	0.53	−0.26
Isle of Man	24	23	1.04	—
Shetlands	14	7	2.0	—
Färöer	9	3	3.0	—
Island	6	2	3.0	—

the Hamburg* region as the continental region of comparison (Stern, 1926;
330 Franck, 1928). After some corrections** and after excluding the anthropobionts *Pristonychus* and *Sphodrus* we obtain a list of 298 species. The "inconstant macropterous" element ("b + d" in Tables 10, 25) comprises 81 species (27%) and is divisible into 33 more or less pronounced larval hibernators ["O + L + (L)," Tables 13, 26] and 48 predominantly imago hibernators. The index number for the region of comparison becomes 0.69, much higher than for any of the North Sea islands except Helgoland.

The unparalleled lowest value is shown by Memmert, the youngest of the islands considered in the present work; its youth is evident from the small number of flightless species (Table 25). But the small number of larval hibernators is not characteristic of every young island. On the contrary, Gotska Sandön has a *high* index number being unique in Fennoscandia. We took this (p. 285) as proof that the flightless element reached this island mainly *in summer*. Conversely we now seem to be justified in assuming that transport of flightless

*Hamburg area or Devon, England.

**Following Horion (1941), these species have been excluded: *Acupalpus longicornis* Schaum, *A. luteatus* Dft., *A. suturalis* Dej., *Agonum viridicupreum* Gze., *Amara tricuspidata* Dej., *Bembidion distinguendum* Duv., *B. fluviatile* Dej., *B. testaceum* Dft., *Harpalus flavicornis* Dej., *Pterostichus interstinctus* Sturm, *Trichotichnus laevicollis* Dft.; those not rating species status are *Amara convexior* and *A. silvicola.* On the other hand the following species, which were considered mere "varieties," are good species: *Agonum moestum, Bembidion properans,* and *Dromius nigriventris.* Among the species that were not mentioned earlier, the following are brachypterous: *Abax ovalis* Dft., *Carabus auronitens* Fbr., *C. variolosus* Fbr., *Harpalus autumnalis* Dft. (according to specimens from Oderberg in Mark Brandenburg), *Pterostichus inaequalis* Marsh. (Kult, *in litt.*). *Abax* and *Harpalus* are included as larval hibernators, with reservations.

species to the Frisian islands takes place chiefly during the *winter half-year*. Palmén (1944, pp. 155 ff.) has shown that the high saline content of the sea has a very deleterious "desiccative" effect on most coleopterans, and besides that hydrochorous transport at low temperature is far more easily endured. There is a possibility of insects being passively dispersed with ice-floes in winter off the German North Sea coast. The rivers are flooded at this time of the year, which accelerates passive dispersal beyond their estuaries and sweetens the water there. —If these conditions are not met on true oceanic islands (Helgoland, Scilly), imago hibernators are not favored, whereas immigration of flightless species proceeds very slowly and these islands, though not young, are characterized by a great preponderance of flying forms. Finally, islands
331 whose fauna is older than postglacial (Lundy, Shetland, Färöer, Iceland) are unaffected by these factors.

Summary

The following factors have been found to be the most important ones in determining the composition of the insular faunas considered:

1. *Age*. The biological age of an island, as long as it is not older than postglacial (in the broadest sense of the word), has a surprisingly small role in the composition of its fauna. I recall that *Hailuoto*, which is the youngest of all Fennoscandian islands considered, has a fauna of completely normal composition, and also *Memmert* among the East Frisian islands, whose fauna is less than 100 years old yet is conspicuous only in a moderate deficit of flightless species and of larval hibernators. On the other hand, as compared with other outer islands, the fauna of *Hogland* shows a striking "maturity," which is evident primarily in the higher percentage of brachypterous species. To some extent the explanation is possibly to be sought in other characteristics of the biotope, but without doubt the many times greater biological age of Hogland is decisive. The present-day isolation and the possibility of immigration per unit time are considered to be identical for all the outer islands. —However, the actual peculiarities, especially a strong predominance of the flightless element, become evident only if the fauna of an island (from our point of view) is very old, i.e. if it has survived the last glaciation *in situ* (or nearly so). Evidently this has happened during glaciation due to selection having a unilateral effect (cf. the dimorphic species on p. 412). —The biological age of a Fennoscandian island might not go back farther than the last interglacial period in any case; real insular endemics are lacking in our area.

2. *Isolation*. Isolation is the distance from the nearest mainland (or from a larger island). This factor evidently plays a decisive role. The apparently youngest faunas, i.e. the most fragmentary ones, are found on *Gotska Sandön* and the *Finnish outer islands* (excluding Hogland). These show the greatest absolute isolation of all the Fennoscandian islands. And in this respect postglacial conditions have never been as favorable as now. —Conversely the fau-

nas of *Värmdön* and *Orust*, islands not much older but isolated solely by very
332 narrow, riverlike straits, differ very little from those of the respective mainland. Strangely, this goes for *Hailuoto* as well, the youngest of all the Fennoscandian islands considered, separated indeed from the mainland by 9 km of water, but apparently located in a highly favorable spot for a hydrochorous transport.

3. *Previous Land Connection.* The relationship between water and land during the postglacial period (sensu lato) in Fennoscandia is largely characterized by a regression of the sea. Only in the south variations have been so large in this respect that the present-day shoreline does not represent the lowest of the postglacial period. Hence in the Baltic Sea an earlier more favorable position of the shoreline (i.e. the possibility of a postglacial land connection) is conceivable only for islands situated south of an oblique line between southern Ösel, central Gotland and northern Öland. Such a land connection has generally been assumed only for *Bornholm*, moreover for *Ven* on the west coast and often between Öland and the nearest Swedish mainland to the west as well. The faunistic consequences of any such former connection are naturally a closer "affinity" (larger number of common species) between the island in question and the mainland with which it was earlier connected, and moreover a greater representation in the insular fauna of terrestrial animals that are difficult to disperse*. Such (and other) considerations convinced me that *Öland* and *Gotland* would not have acquired their present-day fauna without a firm land connection with the now existing German Baltic Sea coast. For geological reasons such a connection was possible postglacially only during the early Ancylus period. I cannot say anything about Ösel for lack of knowledge of its fauna in this context. —For all the other Fennoscandian islands treated here it may be stated, that postglacially they possessed *no* land connection with the mainland. It is not possible to judge how far an *interglacial* connection between the West and North Norwegian islands and the mainland has influenced their present-day faunal composition.

4. *Winds and Water Currents.* Dispersal of the flying forms is naturally influenced by the prevailing winds. On Åland, corresponding with the more
333 frequently southwesterly winds there, a greater immigration of anemochorous plants might have taken place from Sweden. But in the case of carabids, and possibly other insects in part, the *flight activity* seems to have worked in the opposite atmospheric direction and seems to have been more effective. Moreover the wind conditions in Fennoscandia are so irregular that a clear effect on the dispersal of the animals cannot be expected. An indirect effect of the westerly winds on animals drifting hydrochorously to the south with ice-floes in Åland Hav (outermost part of the Skärgård) has been *assumed.* —Otherwise the sea currents play a decisive role in hydrochorous transport. Favorable currents

*On *Bornholm* the latter characteristic of the fauna is obscured by the large number of accidental migrants, on *Ven* by the almost total transformation into arable land.

connect the eastern Baltics with the *southwestern Finnish Skärgård* (including Åland) and could also have affected the fauna of the islands in the Gulf of Finland. However, it is uncertain whether a transport of animals over such long distances can be generally effective; hence it has been seriously considered only for *Drilus concolor* (in view of the peculiar biology of the species). The influence of hydrochorous transport by sea might be greatest in spring when there is drifting ice. Of a totally different kind is the fresh water debouching from the estuaries of rivers, whose high transportation effect, particularly during spate at the time of the ice break-up, extends far beyond the estuarine region. This transport has certainly been very important for the colonization of *Hailuoto*. In seas of high saline content there is, in addition, a sweetening of the water outside the river estuary, so the animals are in a better position to withstand the distress at sea. This is primarily true for the Frisian islands (for instance Memmert), besides also possibly for Hvaler and the Skärgård of Göteborg.

5. *The Role of Man.* On the one hand man has greatly altered the original island biotope (most distinctly on the Island of Ven) by cultivation and drainage of soil, deforestation, etc. On the other hand trade and commerce provide opportunities for the introduction of new species. There has evidently been anthropochorous immigration to all the islands inhabited by man. This may be particularly evident on *Ven* and on the islands of the *Skärgård of Göteborg.* But its importance seems to have been generally over-rated, as discussed elsewhere (p. 606). Quite isolated islands or ones almost untouched by man, such an *Nordfuglöy* and others belonging to the outer skerries of western and northern Norway, as well as Memmert among the Frisian islands, do not
334 show a greater deficit of flightless species (which would indeed be exceedingly dependent on anthropochorous passive dispersal) than what could have been expected in respect to their age, isolation, etc.

6. *The Dynamic Properties of the Insects.* The capability or inability for flight is decisive. The division of the fauna of every island into these two dynamic groups is the basis of this whole study. Since the flightless forms are dependent chiefly on hydrochorous immigration or on passive dispersal by man they must be considered as especially difficult to disperse. And the presence of this faunal element, which only rarely includes accidental migrants, must be significant for the island concerned. —However, in considering the fauna of Åland, special attention was devoted to the flying forms as well. It was experimentally shown that at least certain species do not have directionless flight, but on the contrary show an inclination to fly toward the sun. Since flight is commoner in the afternoon and evening than in the first half of the day it often resulted in a deviation *toward the west.* It has been seen that this phenomenon holds not only for Åland but also for Gotska Sandön, Fårön, Gotland and Bornholm. The general consequences are considered later (on p. 592).

A study of the insular faunas provides valuable information on how a

species usually expands its area. The general conception might be that every dispersal across the sea proceeds more slowly than overland. But, I do not believe that this is true without further ado. In my opinion the main points of Palmén's (1944) conclusions on the importance of anemohydrochorous transport are correct, i.e. a subsequent hydrochorous phase, in comparison with purely anemochorous passive dispersal, means a higher safety during colonization; hence rapid expansion of the area occurs easier across small maritime basins than over stretches of land comparable in size. Thus islands that are more or less close to the mainland are even more favorably situated than the mainland itself for the immigration of an element capable of flight, but are of course unfavorably situated with regard to the soil-bound element.

Wing Dimorphism

An Example of the Zoogeographical Influence of Time

335 Wing dimorphism (J. Sahlberg, 1868) is understood as a phenomenon in which within one and the same species there are some *macropterous* individuals (long-winged and usually capable of flight; "+ winged"), and some *brachypterous* individuals (short-winged, flightless; "– winged"). In the case of the aquatic Hemiptera *Aphelocheirus,* Larsén (1931, p. 10) distinguishes between brachypterous and "micropterous" individuals (the latter with still smaller wings), and in addition uses the terms "hypobrachypterous" and "hypomacropterous". It appears practicable to designate forms with generally reduced wings as *brachypterous* (or micropterous) (true apterous forms might occur among Coleoptera only in the case of certain females, for instance those of *Lampyris*), and to designate as intermediate all possible transitional forms between these and the *macropterous* form. In case of need, these may be called *forma intermedia* a, b, c, etc. A more definite terminology would be unsuitable in view of the highly different grades of intermediates in different species. In cases where such intermediate forms occur it is more correct to speak of *polymorphism*. A pronounced dimorphism or polymorphism with respect to the wings occurs only among insects.

Wing dimorphism associated with sex has evoked particular interest. In such cases the female is generally brachypterous or even apterous (no trace of wings), yet the male fully winged. Well-known examples are: *Blatta orientalis* L.; certain Corrodentia (Copeognatha); Microphysidae; *Orgyia*, *Operophthera*, (*Cheimatobia*), *Erannis*, *Biston* and other Geometridae, Psychidae, *Exapate*; Strepsiptera; *Drilus*, *Lampyris*, *Rhipidius*, *Duliticola*; *Clunio*; Mutillidae, numerous Proctotrupidae, Hecabolinae, Gelidini, and other Cryptinae. —Very rarely is the male brachypterous (or apterous) and the female fully winged: some Thysanoptera; *Xyleborus* (*Anisandrus*); *Blastophaga*, *Prestwichia*, *Alloea*.

336 In some cases only one sex shows wing dimorphism, such as in females of the species of *Chloriona* and *Euidella speciosa* Boh.; several Thysanoptera; *Eupelmus*; *Lycia hirtaria* L. (Nordman, 1946, p. 111); some Aphididae and Cynipidae, associated with the alternation of generations; in males of Coccidae and in *Capnia*.

Wing dimorphism in Carabidae, however, is not associated with sex. In none of the species where sufficient material was available was it found that a particular wing form was common to one sex rather than the other.

This *asexual wing dimorphism* is especially common in Coleoptera and Hemiptera. The following genera may be mentioned as examples of the former group: *Arpedium* (Munster, 1933), *Lathrobium* and *Paederus* (Eppelsheim, 1879), *Mycetoporus* (Hellén, 1925), *Stenus*, *Cherysomela* (Rüschkamp, 1927), *Longitarsus* (Kolbe, 1921, p. 400), and *Sitona* (Jackson, 1928), and the family Ptiliidae (Kolbe, l.c., p. 399).

Among the Hemiptera there are a large number of aquatic species, particularly in the families Corixidae, Naucoridae, Gerridae, Veliidae, Hydrometridae, Hebridae, Mesoveliidae (see Larsén, 1930, 1931), but there are also terrestrial Heteroptera, for example, in the families Capsidae, Anthocoridae, Nabidae, Tingididae, Lygaeidae (see, among others, J. Sahlberg, 1868; Håk. Lindberg, 1929); also numerous Cicadina, particularly in the families Jassidae and Araeopidae (Delphacidae) in which several genera invariably exhibit dimorphism. Asexual wing dimorphism is also shown by various Orthoptera Saltatoria (Chopard and Bellecroix, 1928; Klingstedt, 1939, p. 8; Ander, 1947), Blattidae (Chopard, 1932), and Thysanoptera.

A peculiar form of asexual wing dimorphism is shown by the Neuroptera *Psectra diptera* Burm., in which there are individuals of both sexes with or without reduction of hind wings (for example Tjeder, 1936).

That wing dimorphism in the family Carabidae is such a widespread phenomenon was not hitherto known. Only in the eastern USA has the carabid fauna been studied for this character in some detail (Darlington, 1936). The condition of the wings has been conspicuously neglected by European carabid taxonomists, even in modern monographs (with the exception of Jeannel, 1926–28). Actually the older authors often provided more precise information in this regard, such as Paykull (1798), Gyllenhal (1810–27) and Zetterstedt (1840). This was because they considered wing formation as an important tax-
337 onomic character, and in their keys generally divided the species into "apteri" and "alati". Therefore, already Paykull (1798), for example, was able to recognize the wing dimorphism in *Cymindis vaporariorum* (p. 122, "*humeralis*") and *Olisthopus rotundatus* (p. 136)*. A survey of this phenomenon was offered by Verhoeff (1891b) on *Calathus*, by Oertel (1924) on *Carabus*, and by Sharp (1913) and Maran (1927) on *Pterostichus*. A historical account is omitted here.

338 There are thus almost exactly as many dimorphic species as consistently brachypterous species (49) in the region (p. 573).

*On the other hand his statements must be incorrect for *Patrobus atrorufus* (p. 123, "*excavatus*") and *Calathus ambiguus* (p. 165). This is due to confusion, in the former case possibly with *P. septentrionis*, and in the latter case undoubtedly with *C. erratus*.

Some species will certainly be added to the list in Table 27 when, for instance, sufficient material of certain other carabids is examined. For example the variability of the moderately reduced wings in *Agonum ericeti**, *Badister sodalis* and *Elaphrus angusticollis* makes it highly probable that fully-winged individuals of these species also occur. Likewise among the normally macropterous species, *Bembidion pygmaeum* and *Pterostichus nigrita*, for instance, show variation in the size of their wings, indicating that they are perhaps not constantly capable of flight. According to Letzner (1847–52, pp. 153, 155), *Dolichus halensis* and *Sphodrus leucophthalmus* are dimorphic in Central Europe, but this needs to be confirmed.

The total number of dimorphic species found in Fennoscandia is thus 50 (species that occur in both forms within the area). They constitute 13.8%
339 of the entire fauna (362 species). In the eastern USA, Darlington (1946; see also Lindroth, 1939, p. 258) originally found that 2.2%** of the carabids were dimorphic, a figure which he later (1943, p. 41) could raise up to 4%. Comparisons with other parts of Europe are not yet possible. Although much less material was available to Darlington than to me it is surely not too much to say that *Fennoscandia has an unusually large number of species showing wing dimorphism*. An important task will be to find the underlying reasons.

In most cases there is true dimorphism, i.e. the macropterous and brachypterous forms are not linked by intermediate forms (Figs. 24, 25). The greater the difference between the two extremes, i.e. the smaller the wing rudiment of the brachypterous form, the more this appears to hold true. If occasional intermediate forms do appear they often have more or less asymmetrically formed wings and are to be considered monstrosities. Their pronounced rarity is clear from the following two examples: Among hundreds of individuals of *Calathus melanocephalus* only one intermediate specimen was found (Skå Höllviken), and only one intermediate specimen out of 1,478 individuals of *Bradycellus collaris* (Jtl Revsund). There is an unusual case of one specimen of *Agonum obscurum* from Al Finström (Forsius, MH!), whose left wing is fully developed while the right wing is reduced to a small scale. However, the rudiment is larger than in normal brachypterous specimens and is moreover somewhat irregularly formed, thus probably resulted from damage in the pupal stage. A similar specimen of *Platynus retractus* Lec. was described from North America by Darlington (1936, p. 146).

There is no sharp line of demarcation between true dimorphism and more or less pronounced polymorphism of the wings. As already mentioned, the less

*The assumption that *Agonum ericeti* is dimorphic, at least in southerly areas, was later confirmed (see Supplement).

**Not 2.4% as mentioned earlier (Lindroth, l.c.). This is because among the polymorphic species Darlington (l.c.) included *Micromaseus corrusculus* Lec. (p. 144), of which no fully winged individuals were observed; this species therefore broadly corresponds with *Badister sodalis* of our fauna.

337 **Table 27. Fennoscandian carabids showing wing dimorphism (including polymorphism)**

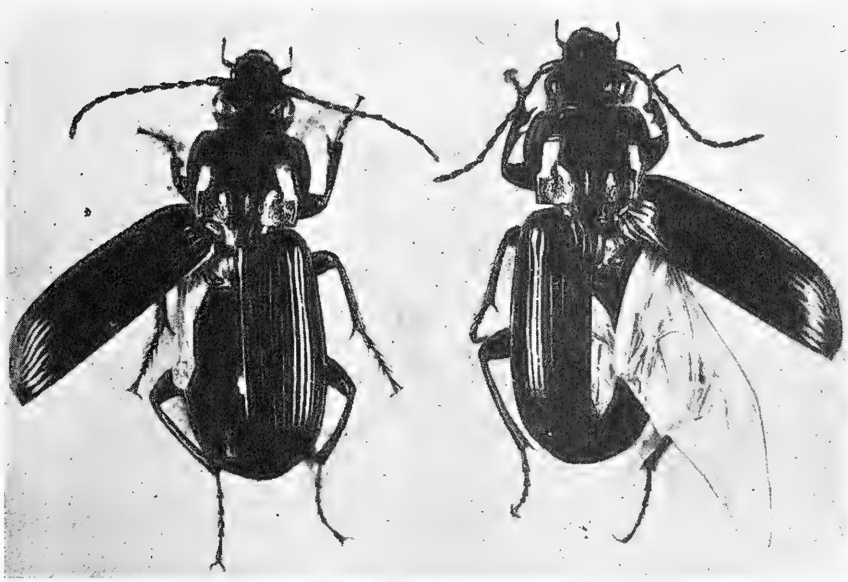
Species in parentheses are found within the area only in one form (m—macropterous; b—brachypterous).
Species with asterisk (*) are the ones whose macropterous form has been observed flying.

		Agonum fuliginosum		*Drominus linearis*
	*	*A. moestum*		(*D. melanocephalus*) m
		A. obscurum		*D. nigriventris*
		(*Amara curta*) m		*D. signa*
		A. infima		*Harpalus azureus*
		(*A. quenseli*) m		*H. neglectus*
	*	*Bembidion aeneum***	*	*H. picipennis*
	*	*B. assimile*	*	(*H. smaragdinus*) m
		B. clarki		(*Leistus ruformaginatus*) m
		(*B. dauricum*) b		*Masoreus wetterhalli*
		B. gilvipes	*	*Metabletus truncatellus*
		B. grapei		*Microlestes maurus*
		B. grapeioides		(*Nebria gyllenhali*) m
	*	*B. guttula*	*	*Notiophilus aquaticus*
	*	*B. lampros*		*N. biguttatus*
		B. nigricorne		*N. germinyi*
	*	*B. obtusum*		*N. palustris*
		B. properans		*N. reitteri*
		B. schüppeli		*Olisthopus rotundatus*
		B. transparens	*	*Pterostichus anthracinus*
	*	*B. ustulatum*		*P. diligens*
	*	*Bradycellus collaris*		*P. lepidus*
		B. harpalinus		*P. minor*
	*	(*B. similis*) m	*	(*P. niger*) m
	*	(*Calathus ambiguus*) m	*	*P. strenuus*
		C. erratus		*P. vernalis*
		C. melanocephalus		*P. vulgaris*
		C. mollis		*Synuchus nivalis*
		(*C. piceus*) m	*	(*Tachys bistriatus*) m
	*	*Carabus clathratus*		(*Trechus fulvus*) b
338	*	(*C. granulatus*) b		(*T. obtusus*) b
		Cymindis macularis		(*T. quadristriatus*) m
	*	*C. vaporariorum*		*T. rivularis*
	*	(*Demetrias monostigma*) b		Total 50 (+ 17) species

** In the case of *Bembidion aeneum* individuals from macropterous as well as mixed populations have been observed flying.

rudimentation proceeded in the brachypterous form, the more frequent the latter condition. In cases where even the wing rudiment has a well-defined stigma along with the succeeding reflexed apical part, it is at first not easy to establish the macropterous, i.e. the flying form and, at times, to determine the occurrence of dimorphism or polymorphism at all. In this connection difficulties are encountered especially in the case of *Agonum moestum*, *Bembidion aeneum*,
341 *Calathus erratus*, *Microlestes maurus*, *Pterostichus vernalis,* and *Synuchus*. Intermediate forms are also often found in *Bembidion grapei*, *B. grapeioides*, *B. guttula*, *B. transparens*, *Pterostichus minor*, and *P. strenuus*; in *Olisthopus* I have so far seen only 3 intermediate specimens (4 Lillesand, MO!). In certain cases the classification of individuals into groups by wing size seems to form a continuous series, as Palmén found (1944, p. 146) in 400 specimens of *Calathus erratus*. (*Carabus granulatus* in Central Europe; Oertel, 1924, pp. 57 ff.).

Considering the family Carabidae as a whole, one gradually realizes, however, that no individual is capable of flight whose hind wings do not exceed the elytra not only in length but also in width. Applying this experience to dimorphic and polymorphic forms will make it possible to distinguish the macropterous form, the only one capable of flight. I would especially like to



340 Fig. 24. *Pterostichus anthracinus*. Brachypterous and macropterous female from Upl Djursholm, Ekebysjön lake. (Photo: I. Stjerna).

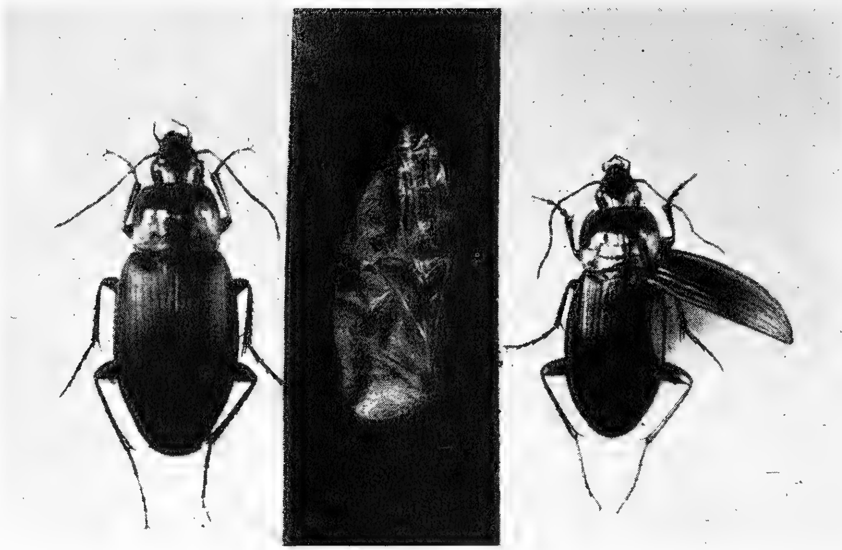
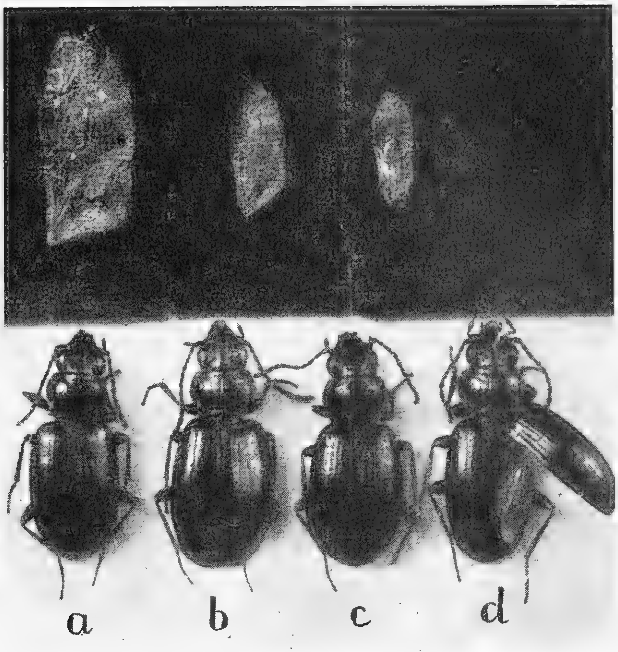


Fig. 25. *Calathus mollis*. Macropterous female and brachypterous male from Skå Södra-Sandby, Skatteberga. (Photo: O. Ahlberg).

emphasize that in the zoogeographical context, as in the present case, not
342 morphological but physiological considerations are decisive: It is important to distinguish between individuals capable of flight and ones that are flightless in order to enable the preparation of survey sheets. From *this* viewpoint there is no difference between dimorphic and polymorphic species, so in the following account I include the more or less pronounced polymorphic species under the term "wing dimorphism." Otherwise, strictly speaking, it would have been more correct to speak of "diphysism" (Klingstedt, 1939, p. 12).

The frequency ratio as between macropterous and brachypterous forms in the dimorphic species varies strikingly from species to species and from region to region. From our point of view the extremes are such dimorphic species that occur only in *one* form in Fennoscandia (see list above); also *Bembidion*
343 *ustulatum* and *Bradycellus harpalinus*, of which in each case only one specimen each of the macropterous and brachypterous form was observed in our region. Only one macropterous individual each is known in the case of *Drominus sigma*, *Notiophilus germinyi*, and *N. reitteri*. In *Agonum moestum*, *Bembidion grapei*, *Harpalus picipennis* and *H. neglectus* there is a great preponderance of the macropterous form. In most other species the contrary is the case. Hence in nature there is no common pattern of "equilibrium" between the



341 Fig. 26. *Bembidion transparens*.

a—Macropterous specimen, Upl Hjälstaviken; b—Intermediate specimen, Upl Dannemora; c and d—Brachypterous specimens, Upl Hjälstaviken. (Photo: O. Ahlberg).

two wing forms, at any rate not in Fennoscandia. Here, as elsewhere, study of the material must take into account the fact that each species presents its own problem.

Causes of Wing Dimorphism

The origin of wing dimorphism in carabids is not readily explicable. Although a dependence on *hereditary factors* is obvious, the influence of environmental factors cannot be rejected out of hand.

That the problem is fairly complex, is evident from the comparatively few studies so far carried out on other insects. Obviously these studies are best known in *Drosophila*. In this genus a whole series of genetically determined wing reductions (mutations) are known, through combinations whereof all transitions from well developed wings to almost total absence of wings can take place (for example, Goldschmidt, 1938, p. 57, Fig.). It is very inter-

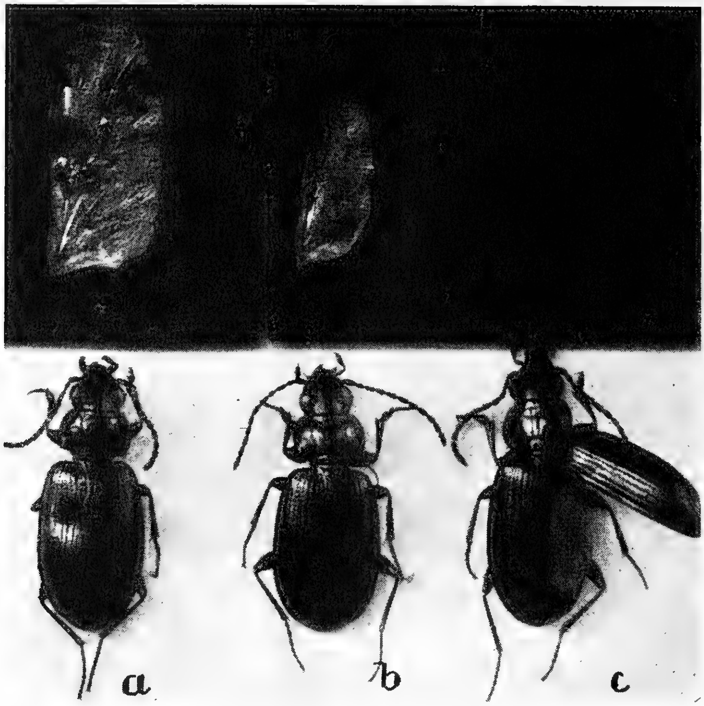


Fig. 27. *Bembidion aeneum.*

a—Macropterous specimen, Vgl Göteborg; b—Intermediate specimen, Boh Bullaren; c—Brachypterous specimen, 31 Bodö. (Photo: O. Ahlberg).

esting that genetic and morphological mutations wholly corresponding with each other, including those concerning the wings, have been observed in *different* species of *Drosophila* (for example, Sturtevant, 1940, p. 343). Hence it is tempting to consider the wing reduction occurring in so many carabids (and other Coleoptera), provided it is genetically determined, as an expression of a "homologous series in variation" (Vavilov, 1922).

Of particular importance are the conditions found by Jackson (1928) in the curculionid genus *Sitona*, namely in *Sitona hispidulus* Fbr., as a result of very careful studies. This case completely corresponds with most of the dimorphic carabids, involving a species that occurs in nature in sharply distinguishable macropterous and brachypterous forms. The cross-breeding experiments discussed below in detail revealed a distinct, direct dependence of the condition of the wings on genetic factors.

On the other hand there is no dearth of observations that reveal the clear

influence of *environmental factors* on the condition of the wings in different
344 insects. In *Drosophila*, among others, Goldschmidt (1938, pp. 4 ff.) treated the larvae with temperature shock and x-rays which caused different modifications in the adult flies, some of which were identical with known mutations responsible for morphological (phenotypical) modifications. He succeeded in obtaining such "phenocopies" for the characters of the wings too. Wing modifications in other Diptera as well as in Hymenoptera were also experimentally produced by Dewitz (1917).

Moreover we know that a wing mutation, such as the well-known "vestigial" (*vg*), varies with temperature in the extent of development. The wing rudiments are larger at higher temperatures (Roberts, 1918; Harnly, 1930). J. Sahlberg (1868) and Håk. Lindberg (1929) believe that low temperatures encourage the development of brachypterous Hemiptera. —In the aquatic bug *Aphelocheirus*, Larsén (1931) showed a clear correlation between wing development and the oxygen content of water.

Mention must also be made of Uvarov's (1921) so-called *phase theory* (see Klingstedt, 1939). It explains the occurrence of "solitary" and "migratory" forms (among other things being related with the different formation of hind wings) in one and the same insect species under the influence of environmental factors, namely population density. Uvarov (1921) based his theory on *Locusta migratoria*, and then gradually, no doubt correctly, extended it to the entire group of Orthoptera Saltatoria (Klingstedt, l.c., p. 9). —It is possible that wing dimorphism in other orders of insects also pertains to the "phase type," but the attempt by Klingstedt (l.c.) to apply the theory of *Gerris asper* (Ekblom, 1927–28) seems to have been invalidated by crossing experiments carried out later on a larger scale with the same insect (Ekblom, 1941)*. —Palmén (1944, pp. 148–149) tried to rear larvae of *Calathus melanocephalus* "in as high a
345 population density as possible" to determine the possible influence thereof. However, the adults obtained (33 specimens) were all brachypterous like the parents.

So it is clear that with regard to the development of wing dimorphism in insect there is no consensus. This is of course because the phenomenon as a whole is not consistent.

The necessary rearing experiments had not been carried out in the case of carabids. I therefore looked for a suitable dimorphic species but at first, with *Bradycellus collaris*, I had little success. It was difficult to obtain vir-

*The results of crossing experiments by Ekblom (1941) make sense only on the assumption of a genetic basis for the wing condition. The mechanisms involved are apparently of an intricate nature. Calculation of the frequency of the "forma *microptera*" in the crosses (No. 1, 9, 10, 12, 14, 17), in which they occurred in F_1, without being represented in the parents, gives a ratio of 1 : 63.5, which is very close to 1 : 64. Thus there are probably three pairs of factors, all of which affect the wings, and the "macropterous" form would then be a recessive homozygote. The most interesting cross would be between two such micropterous forms.

gin females, and since they emerge in autumn I tried repeatedly—without success—to keep such immature females through the winter. Experiments with *Calathus erratus, Pterostichus vulgaris* and others were also unsuccessful. Finally by chance I got dimorphic material of *Pterostichus anthracinus* (Fig. 24), with which it was possible to undertake the crosses described elsewhere (Lindroth, 1946).

The number of offspring obtained in the F_1 generation was not large, consisting of 52 specimens distributed over 7 crosses. But luckily the most important cross, that between two (evidently heterozygous) brachypterous forms, resulted in an F_1 generation of 25 specimens (13 males, 12 females), of which 18 were brachypterous and 7 macropterous, i.e. approaching the simple Mendelian ratio of 3:1.

The following conclusions drawn (l.c.) were:

1. Wing dimorphism in *Pterostichus anthracinus* is genetically determined.

2. Brachypterism is the dominant character. *The macropterous individuals are therefore homozygotic.*

3. Heredity follows the simple Mendelian ratio.

The important question arises whether the phenomenon of wing dimorphism in carabids as a whole belongs to the same type. Although, strictly, each case should be tested by breeding experiments, it might not be too bold to adopt such an assumption as a working hypothesis, for the following two reasons:

First, the results with *Pterostichus anthracinus* entirely correspond to those obtained by Jackson (1928) on much larger material (with a progeny of nearly 500 specimens) of *Sitona hispidulus*. And when two beetles, a carabid and a curculionid, which are as little related to each other as possible, have been in-
346 vestigated with similar results, then it is natural to presume that asexual wing dimorphism in beetles is in general a consistent phenomenon. —In *Bruchus quadrimaculatus* Fbr. (Breitenbecher, 1925, 1926) a *recessive* brachypterous mutant was indeed discovered (similar cases have been reported in *Habrobracon* by Whiting, 1926, as well as in *Drosophila*), but in the case of *Brachus* a distinctly abnormal form was involved, which showed vestigial elytra as well. Moreover this mutation occurred phenotypically only in the female, thus was evidently of an entirely different nature, other than the asexual wing reduction in carabids.

Second, the regular geographical distribution of the two wing-dimorphic forms of most carabid species within the Fennoscandian Region shows that the causes of dimorphism follow a regular pattern at least in the majority of cases and are always the same. The distribution maps, discussed below in detail, are understandable only on the assumption that *the macropterous individuals are recessive homozygotes.*

A special problem is posed by the very few more or less *polymorphic species*. Their genetic conditions can be clarified only by breeding experiments.

But it is already certain that the intermediate forms are not simple heterozygotes, since they occur more rarely than the two extremes. Yet in certain cases they are more frequent within limited populations. Among 12 individuals of *Pterostichus strenuus* from 32 Saltdal, 10 belonged to a uniform intermediate type (the other two were normal brachypterous specimens). The assumption of a different, secondary mutation is obvious. It is easy to imagine a polymorphic series arising by the combination of a relatively small number of wing-reducing mutations (Goldschmidt, 1938, p. 57; Jackson, 1928, p. 729). On the other hand the influence of environmental factors on the external structure of the wing rudiment (cf. "*vg*" in *Drosophila* mentioned above) cannot be dismissed. When preparing the survey sheets, the problem of the polymorphic species was solved by designating all individuals as "brachypterous" whose wings were normally not fully developed. In this way the flying individuals were without doubt separated from the flightless ones (except some individuals with abnormally rudimentary wing musculature), which appeared to be the most important task in the present context. Presumably, future studies will show that this division corresponds to a genetic division as well.

347 The possibility of repeated ("recurrent") mutuations in separate populations of the same species is discussed below (p. 393).

From the general evolutionary viewpoint it is significant that a big reduction of the hind wings can take place in a single step, *by a single mutation*. In this connection the vague discussions on orthogenesis and the "use or disuse" of an organ are totally unnecessary (Kolbe, 1921, pp. 403–404, 407; Rüschkamp, 1927; Meixner, 1934, p. 1084), as well as discussions on a phenomenon comparable with neoteny (Jeannel, 1925, p. 1224; 1940, p. 78). —Macropterous individuals of no less than 25 of the dimorphic species listed above (Table 27) (including *Pterostichus anthracinus*) have been observed flying. Evidently the important thing is not the loss of the habit of flying but the appearance of the wing-reducing mutation.

Other Characters Associated with Wing Reduction

It is rarely possible to distinguish the brachypterous form of a carabid from the macropterous form without examining the hind wings, that is, by raising the elytra. Exceptions are provided by some (but not all!) individuals of *Bembidion grapei*, *Pterostichus anthracinus*, and *P. vulgaris*, which have shorter, flatter and laterally more rounded elytra. Corresponding with this, other authors have reported that alterations in certain morphological characters of a beetle appear to have a more or less regular parallel in the wing reduction (see also Jacobson, 1889).

Most of the morphological peculiarities on the basis of which the brachypterous species of beetles and perhaps also brachypterous forms of the dimorphic species can be separated from the macropterous ones,

have a distinct functional correlation with the loss of flight capacity. Such morphological peculiarities are:

a. Reduction of Flight Muscles

Jackson (1928, pp. 679 ff.; 1933), who carried out anatomical studies on extensive material of *Sitona hispidulus*, showed that reduction of the wings and of the flight muscles are not always concomitant. There are macropterous individuals with greatly reduced flight muscles and brachypterous individuals with almost fully developed flight muscles. (Furthermore, the flight muscles may undergo reduction during adult life.)

Similar conditions are also known in *Hemiptera*, especially in the aquatic forms (Poisson, 1924, 1925; Larsén, 1947). These animals also exhibit the rare
348 combination of reduction of the wings and retention of the flight muscles (see especially, Poisson, 1925).

The effect of wing-reducing mutations on the flight musculature is still less in *Drosophila*, in which it seems to remain unaffected, even in the case of the phenotypically effective mutation "no wings" (Cuénot and Mercier, 1923).

Study of the flight muscles of 14 specimens of *Pterostichus vulgaris* from Dlr Lima (preserved in strong alcohol) showed that these were much reduced in all of the 10 brachypterous specimens. Of the 4 macropterous specimens, 3 had well-developed flight musclature and were certainly capable of flight, but in the fourth individual these muscles were just as rudimentary as in the brachypterous specimens. One difference is, among other things, in the two *musculi metathoracis mediani* (nomenclature according to Bauer in Korschelt, 1923, p. 574), which either consist of three strong, distinct fibrous bundles each or are reduced to hardly visible rudiments. —In the material of *Pterostichus anthracinus* from Upl Djursholm, Ekebysjön lake, though badly fixed, the flight musculature seems to be equally well developed in both forms.

b. Reduction (particularly Shortening) of the Entire Metathorax

This is a secondary phenomenon, evidently a consequence of reduction of the flight muscles. This may manifest especially in the following ways: Weak chitinization of the metatergum (for example, in *Sitona*; Jackson, 1928, p. 674); rounded off shoulder region of the elytra (frequently found in all constantly flightless Coleoptera, for instance, Curculionidae, but not without exceptions; not noticeable in *Sitona*); and shortening of the lateral parts (metepisterna) of the metathorax.

The last-mentioned change is usually evident from comparison of macropterous and brachypterous *species* of the same genus (Mařan, 1927, pp. 135–136). It has even been used as a character for separating the species *Calathus melanocephalus* and *C. mollis* (for example, by Ganglbauer, 1892, p. 245). Both species yet are nevertheless dimorphic, although the macropterous form of *melanocephalus* is very rare (11 specimens out of

380 from Fennoscandia). Gersdorf (1937, pp. 81–82) unsuccessfully tried to separate the two species on the basis of the relationship between the length and width of the episterna, which is not surprising. My own measurements gave the following index values:*

349 *melanocephalus* 5 macropterous specimens (from Små, Ång, Nbt, Pil, Lul): 1.42, 1.54, 1.67, 1.71, 1.71. .... Mean 1.61.

melanocephalus 5 brachypterous specimens (from the same provinces as above:) 1.44, 1.63, 1.64, 1.68, 1.73. .... Mean 1.62.

mollis 10 macropterous specimens (from Skå, Ble, Små, Öld, Gtl): 1.62, 1.67, 1.71, 1.76, 1.80, 1.82, 1.82, 1.82, 1.89, 1.91. .... Mean 1.78.

mollis 10 brachypterous specimens (from the same provinces as above): 1.42, 1.50, 1.54, 1.55, 1.56, 1.64, 1.64, 1.65, 1.66, 1.68. .... Mean 1.58.

Hence a clear correlation between the development of the hind wings (probably more correctly of the flight musculature) and that of the metepisterna is found only in *C. mollis*. Corresponding to this, the curve for "stretched, uniformly brown insects" (= *mollis* p.p.) in Gersdorf is slightly bimodal. Mařan's contention (1927, p. 136) that in *C. melanocephalus* too the relative length of the metepisterna varies according to the development of the hind wings, could be based on a confusion (of that species)† with *C. mollis*.

Like *Calathus melanocephalus*, in *Pterostichus anthracinus* and *P. vulgaris* there is no demonstrable difference in the structure of the metepisterna between macropterous and brachypterous individuals. In the latter species the following index values were obtained with 10 specimens of each of the two forms (from Boh, Nke, Dlr, Ång, Vbt):

macropterous form 1.97, 2.0, 2.0, 2.0, 2.03, 2.05, 2.06, 2.06, 2.11, 2.13 .... Mean 2.04.

brachypterous form 1.88, 1.89, 1.94, 1.95, 2.0, 2.0, 2.0, 2.08, 2.12, 2.13 .... Mean 2.00.

This correlation is strange, since the flight musculature of the brachypterous form of *P. vulgaris* seems to be constantly rudimentary (see above). One would like to imagine that the structure of the metathorax should automatically adapt to the size of the flight muscles. Where, as here, this is not so, it must perhaps be assumed that the size of the metepisterna is regulated by a particular gene.

c. Reduction or even Loss of Humeral Callus on the Elytra

This feature has often been used by the systematists (for instance, by Jacobson, 1899) as characteristic of short-winged *species*. For the brachypterous *individuals* of a dimorphic species this is characteristic of the genus *Lon-*

*That my values are consistently higher than Gersdorf's is due to the fact that in measuring the length I included the epimera, which are fused with the tip of the episterna.

†(suppl. translator).

350 *gitarsus* (Kolbe, 1921, p. 401). Among the dimorphic carabids I am aware only of cases where some (not all) brachypterous individuals are conspicuous by a somewhat narrowed shoulder region (for instance, in *Bembidion grapei, Pterostichus vulgaris*).

d. Fastening (Ankylosis) of the Elytra along the Suture

In constantly brachypterous species, especially in the families Carabidae and Curculionidae, this is a frequent phenomenon, which has been precisely described and superbly illustrated by Corset (1931, pp. 47 ff.). This does not involve a coalescence but there is a fine longitudinal carina along the margin of one elytron, which fits into an exactly corresponding furrow of the other elytron, where it is firmly anchored (see below p. 575).

This firm fastening of the elytra occurs in none of our dimorphic carabids. However, two species, *Calathus erratus* and *Pterostichus lepidus*, show a similar phenomenon: in the brachypterous form of these species, if one tries to raise the elytra, they often break transversely just behind the scutellum (even in very fresh material). Evidently at this point there is a stronger fastening between the elytra which, as in the cases described by Corset, is due to a fine longitudinal carina on the edge of one (the left) elytron.

It has been observed in the case of the *Calathus* species that this carina varies considerably in width. It also begins more abruptly behind the scutellum in cases where it is broader. The structure of this carina evidently has an important role in raising and spreading the elytra. For the elytra are so firmly anchored in the two sharp longitudinal furrows of the metascutellum immediately behind the scutellum by their turned-down sutural margins, that lateral movements of the elytra are virtually impossible. However, without such movements the elytra cannot be separated, thanks to this carina.

A distinct broad sutural ridge is found predominantly (but not exclusively) in brachypterous individuals of *C. erratus*. However, this correlation must be verified on much more extensive material. It must be experimentally established whether "broad-ridged" individuals are flightless even when they have fully-developed wings.

e. Vestigial Eyes

The association of this character with wing reduction has been shown by Jeannel (1926, p. 278; 1927, p. 303) especially in the cavernicolous and
351 subterranean Trechinae, and even in the central European dimorphic species *Trechus obtusus* (constantly brachypterous in our region). The macropterous form *obtusoides* Jeann., occurring in southern France, Spain and North Africa, has noticeably larger eyes. According to Chopard (1932) a similar state of affairs occur in Blattidae, even in species showing wing dimorphism, which suggests a genetic correlation. Darlington (1932, p. 152) discovered a similar case in the dimorphic carabid *Limnastis americanus* Darl. from Cuba. —This

phenomenon was not observed in the Fennoscandian material.

f. That the psychical functions, being connected with flight readiness, are not always lost with the reduction of wings has been shown by Krogerus (1932, p. 150) in the (probably constantly) brachypterous *Eonius bimaculatus* Ill, Anthicidae.

I have observed the identical case in a brachypterous specimen of *Bradycellus collaris* (Jtl Revsund, September 5, 1947), which on exposure to artificial light performed all the usual preparations for flight: the antennae were thrust forward and swayed uneasily, the legs "marked time," the elytra moved slightly apart, the abdomen made upward directed, pushing movements and the entire body quivered. Suddenly the elytra were jerked up in the usual way in an angle of at least 45° to the body (thus the "*musculi levatores elytrae*" were functional) and the animal attempted to fly, even though the wings were reduced to macroscopically barely visible scales.

In conclusion it may be stated with regard to the other morphological features connected with wing reduction in insects, that reduction of the flight musculature and of the entire metathorax occurs with the greatest regularity. But these characteristics show no complete constancy, neither in species that are constantly flightless nor in the brachypterous individuals of dimorphic species.

Future studies, using extensive material, might clarify whether in certain dimorphic species wing reduction is obligatorily connected with reduction of the flight muscles, shortening of the metepisterna, etc. On the basis of our present incomplete knowledge it can be assumed that these external characteristics do not represent the phenotypic expressions of one and the same gene. On the other hand reduction of the wings and the flight muscles occur so often together, at least among the beetles, that this phenomenon can hardly
352 be definitely explained by supposing that every destructive mutation of the flight musculature is inconsequential because the wings are already unusable.

In all probability a complex of genes is involved which individually are not functionally altogether independent of one another. However, that the influence of environmental factors must not be neglected either has been demonstrated by Jackson (1933) with the flight musculature of *Sitona*.

Influence of Selection

Few biological problems have engendered such controversy as selection. One side ascribes a decisive role in evolution and the other discounts or denies its influence compared with that of mutations. The selection value of smaller or nondemonstrable "advantageous" mutations has evoked particular controversy.

In considering wing dimorphism we are in an unusually favorable position with regard to such selection. It might be difficult to demonstrate a character occurring in natural populations, resulting from a single mutation, having

such high selection value as to inhibit flight due to reduction of the hind wings. Whether selection then exercises a positive or a negative influence is completely dependent on the environment in which the dimorphic population lives. We will be in a position to draw conclusions as to previous alterations in the environment by studying present-day conditions, i.e. the present distribution of macropterous and brachypterous forms within the area of a particular dimorphic species. Hence the theme extends far beyond the limits of the animal species in question.

It is quite understandable why, Darwin (1859, pp. 135–136) attaches such importance to the large number of flightless beetles on the island of Madeira and considers this a good proportion of a "natural selection." Later Jeannel (1925) contradicted this view and cited the example of 8 species of Trechinae from Madeira that are indeed all "apterous," and on the other hand 6 species living on the Canary Islands that are winged with only one exception*. He believes that among the Trechinae absolutely no correlation can be found between insular life and wing reduction; the occurrence of a brachypterous species on an island signifies only that its ancestors were already brachypterous,
353 and this is no evidence for the origin of that species on the island (possibly with the sole exception of the brachypterous forms of *Trechus quadristriatus* occurring exclusively on the Island of Elba).

However, Jeannel's thesis is by no means generally valid. First of all, the faunas of the South Atlantic and Antarctic islands (St. Helena, Tristan da Cunha, Crozet Islands, Kerguelen Islands, etc.; Hesse, 1924, p. 555; Holdhaus, 1927–28, pp. 837, 842; Darlington, 1943; Brinck, 1948) show that the insects of islands of a particular type (small, exposed, permanently isolated) have a strong tendency to wing reduction.

Isolates, in the sense that they are surrounded on all sides by ecologically different regions, also occur in *mountains*, especially on isolated peaks, which in (biologically) old regions, such as in the Alps, often have a considerable number of their own endemic species of Coleoptera (for example Heberdey, 1933). These species almost without exception lead a more or less subterranean existence and are consistently wingless.

An especially close relationship holds between inability to fly and habitat in the case of insular and montane faunas.** Recently Darlington (1943; cf. 1936) again took up this problem, and on a broader basis, with regard to

*However, later on more brachypterous Trechinae were discovered on the Canary Islands (Jeannel, 1936).

**Special cases outside the scope of this study are the faunas of *caves* (Holdhaus, 1932) and those of *deserts*. The high percentage of forms with reduced wings in desert areas may be considered as a secondary phenomenon, assuming that as tight locking as possible (often total ankylosis, as in Tenebrionidae) of the elytra is advantageous because it reduces the loss of water (emphasized among others by Brues, 1903, p. 183). The development of an isolated air pocket in the subelytral cavity may also have a role in temperature regulation.

the carabids. The great importance of his work lies in the fact that Darlington takes into account the ecology of different species and is thus in a position to study the influence of selection *concretely*.

Among the montane faunas, Darlington describes and compares the ones of the eastern USA, the Santa Marta region in Colombia (South America) and the Greater Antilles. He finds the following common trends in the carabid fauna of these regions:

a. Small number of species.

b. Preponderance of "geophilous" (soil-bound) species.

c. A marked predominance of flightless species, including the brachypterous forms of dimorphic species.

The *insular faunas* according to Darlington include the "classic" faunas
354 of Madeira, St. Helena, Hawaii and the Seychelles, and those of two small islands off the east coast and one of the west coast of the USA besides those of Bermuda, the Antilles and the Bahamas, the Pribilof islands and Iceland. In the faunas he found the same three features as the common trends that characterize the montane faunas. Exceptions with regard to the predominance of flightless forms are provided by the flat, tropical (and it may be added, young) islands. But even in the faunas of the other islands, the more mountainous the islands are, the higher the percentage of the brachypterous forms.

In his attempts to explain this character of insular and montane faunas, Darlington is justified in sticking to his selectionist viewpoint. In connection with the problem that interests us here, the increase in brachypterous species and forms, he starts from the sound assumption (more fully substantiated in his work of 1936) that the condition of the hind wings in the carabids is genetically determined. This poses the question: Which common external factors are responsible for the increase of the brachypterous mutants in mountains and on most islands.

A discussion of this problem, essential to our theme, is best based on a division of the possible selective factors involved into two groups:

a. Factors directly dependent on the absence or presence of flight capacity.

b. Factors based on secondary differences between brachypterous and macropterous individuals or species.

1. To take up the latter question first, it may be mentioned that a moderate increase of brachypterous species in mountains and on old islands results from the geophilous species being favored there at the cost of ripicolous and arboricolous species, the latter are predominantly macropterous (Darlington, 1943). This finding is certainly correct. However, it of course cannot explain why the brachypterous *form* of a dimorphic species should perhaps be favored.

It was Darlington's contention, very important for our problem, that in dimorphic species the brachypterous form appears to have greater vitality ("viability"). Above all he presupposes Jackson's finding (1928, p. 708) that in crossing experiments with *Sitona hispidulus* the number of brachypterous indi-

viduals obtained was greater, thus that of the macropterous ones was smaller than theoretically calculated. Combining these crossings (altogether 473 spec-
355 imens), which included both, brachypterous and macropterous progeny (Jackson, 1928, pp. 705, 707), the following figures are obtained:

Empirical figures: 312 brachypterous specimens (= 66%), 161 macropterous specimens (= 34%).

Theoretical figures: 291 brachypterous specimens (= 61.6%), 182 macropterous specimens (= 38.4%).

The error is therefore 4.4% in favor of the brachypterous form. Since the material is fairly large, and since the excesses of brachypterous forms occurred in two-thirds (14 out of 21) of the crosses, it must no doubt be concluded that the brachypterous form of *Sitona hispidulus* has a higher vitality in the earlier developmental stages.

However, it is quite another matter whether this conclusion can be readily applied to the dimorphic carabids. In my experiments carried out with *Pterostichus anthracinus* (Lindroth, 1946), which were much less comprehensive, the right numerical proportions were obtained (in one case one macropterous individual and in the other case one brachypterous specimen too much).

It might be remembered that the very thoroughly studied "vestigial" mutant of *Drosophila* showed greatly reduced vitality. On the other hand, brachypterous specimens of *Gerris asper* L. seem to show higher winter-resistance than macropterous specimens (Ekblom, 1941, p. 53).

Darlington attaches great importance to the assumed greater viability of the brachypterous form of dimorphic carabids, which have "simpler structure, simpler metamorphosis and lower energy requirements" (p. 44). Theoretically one can imagine that in particular, a reduction in the flight musculature (but scarcely in the hind wings as such) and the common reduction of the metathorax signify a "material economy"†, which can be used for other organs or bodily functions. But the flight musculature is not always reduced along with the wings (see p. 347).

A general "comparison of vitality" between the two forms of a dimorphic species has to be carried out *experimentally*. I therefore carried out the following experiments with *Pterostichus anthracinus*. The material used for this purpose was especially favorable. It comprised the F_1 generation of the above-mentioned (p. 345) crosses, whose parents were all collected at the same locality (Upl Djursholm, Ekebysjön lake) from an area of a few square meters. The experimental animals thus all belonged to the same population and had lived in exactly the same environmental conditions from the egg
356 onward. The experiments were carried out simultaneously with macropterous and brachypterous forms; the latter were marked with a drop of zinc-white.

†(Meaning economy of organs; suppl. gen. edit.).

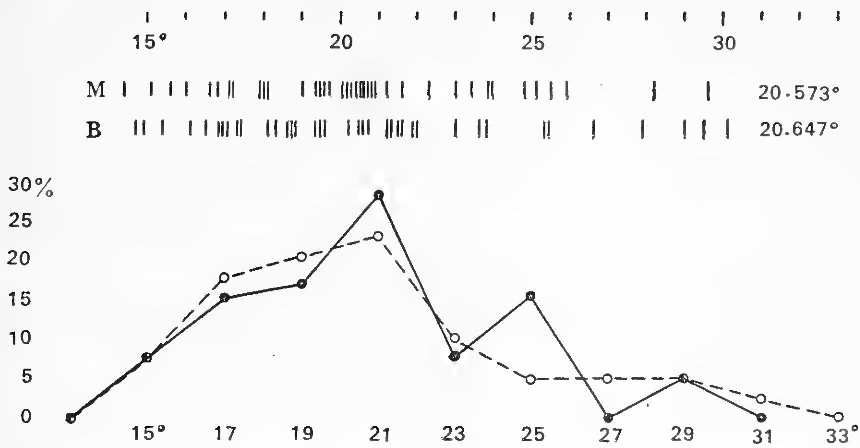


Diagram 43. *Pterostichus anthracinus*, macropterous form ("m"—continuous line) and brachypterous form ("b"—broken line). Distribution in the temperature gradient apparatus and frequency curves. Arithmetic mean values are given on the right. Experiment 26, p. 72.

a. First of all the distribution of each of 38 specimens was studied in the temperature gradient apparatus (Experiment 26, p. 72). The preferendum of different individuals (Diagram 43) at first does not appear to be identical, but an arithmetic calculation of the mean preferenda gives the following values: macropterous 20.573°C, brachypterous 20.647°C, hence a difference of only 0.074°. The statistically calculated mean values are 20.736° and 20.790°C respectively, hence a still smaller difference. The correspondence is
357 as complete as could be hoped for, given experimental error and the relatively small material.

b. The experiments with acidity *preferenda* (Table 28; Experiment 26, p. 77) provided a similar result. Calculated mean values were: macropterous pH 6.22, brachypterous pH 6.39. The material was of course very limited (39 + 39 specimens) in one "alternating" preferendum experiment (see p. 73), but the experiments were discontinued because the species was found to be almost unaffected by the pH in nature (see p. 527).

c. The response to *the humidity of the substratum* was studied (Diagram 44; Experiment 81, p. 80) with more abundant material (100 + 100 specimens).

If we calculate the mean place in boxes (following the 6 box numbers used in the diagram), we obtain the following figures: macropterous 1.82; brachypterous 1.62. To the extent that there is an actual difference, this experiment thus indicates greater attraction of the *macropterous* form toward

356 **Table 28.** ***Pterostichus anthracinus.***

Distribution of individuals of the macropterous and brachypterous form in simultaneous experiments in the substratum gradient apparatus with soils of different pH values. Experiment 46, p. 77

	pH 6	pH 7.5	pH 6	pH 4.8	pH 6
			Specimens		
Macropterous	4	9	11	8	7
Brachypterous	5	10	13	6	5

	Mean	
	Macropterous	Brachypterous
pH 4.8	2.7	2.0
pH 6	2.4	2.5
pH 7.5	3.0	3.3

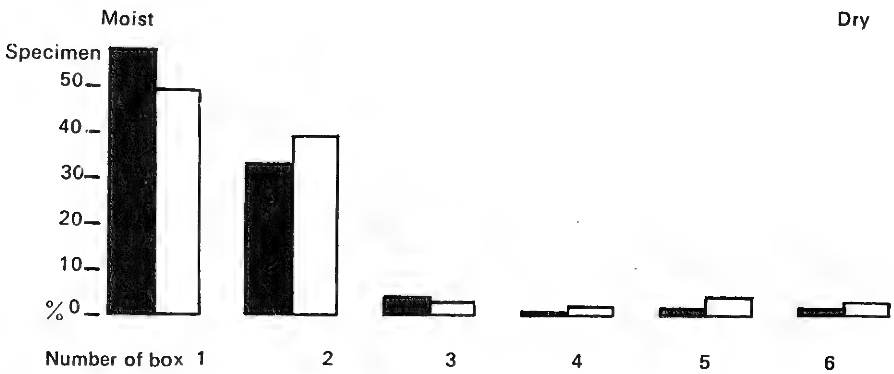


Diagram 44. *Pterostichus anthracinus*, macropterous form (white), brachypterous form (black).

Distribution of simultaneous experiments in the "humidity gradient apparatus." Experiment 81, p. 80.

drier places. From the viewpoint of selection this would probably be a *positive* feature for a hygrophilous species.

Comparative studies were carried out with two other species. In both

cases the macropterous and brachypterous forms came from the same population.

Calathus mollis. Material from Öland, collected as imagines.

358 a. *Lower response point* ("point of turnover of the animals") to temperature (Experiment 128, p. 106)*.

Macropterous form (6 specimens): 6.5, 6.5, 6.9, 7.7, 9.0, 9.1°; mean 7.6°C.

Brachypterous form (3 specimens): 6.9, 8.4, 11.0°C; mean 8.8°C.

359 b. *Resistance to desiccation* (Diagram 45 I; Experiment 140, p. 108). The 8 specimens of the macropterous form showed a mean (maximal) duration of life of 160 hours, the 8 specimens of the brachypterous form, 150 hours.

Bradychellus collaris. Material from Jtl Revsund, collected as imagines.

a. *Temperature gradient apparatus* (Diagram 46; Experiment 7, p. 70). The mean values in the case of the macropterous form were found to be + 12.85°C, both by arithmetic and statistical calculation. For the brachypterous form these figures were respectively +13.46° and 13.7°C. However, the difference lies within the range of variation of both mean values.

b. *Lower response point* ("point of turnover of the insects") to temperature (Experiment 130, p. 106).

Macropterous form (20 specimens): –1.8, + 0.5, 2.3, 2.4, 4.2, 4.8, 5.2, 5.4, 5.4, 6.0, 6.0, 6.2, 6.7, 6.9, 7.4, 7.5, 7.5, 8.9, 9.8, 10.2°; mean 5.6°C (statistically calculated: 5.8°C).

Brachypterous form (20 specimens): –1.8, –1.8, –0.7, + 1.2, 1.5, 2.6, 3.5, 3.8, 4.2, 4.7, 6.6, 7.4, 7.7, 7.7, 7.8, 7.8, 8.2, 9.6, 10.3, 10.8°; mean 5.0°C (also after statistical calculation).

c. *Resistance to desiccation* (Diagram 45 II; Experiment 142, p. 108). 10 specimens in each case gave the following mean (maximal) duration of life:

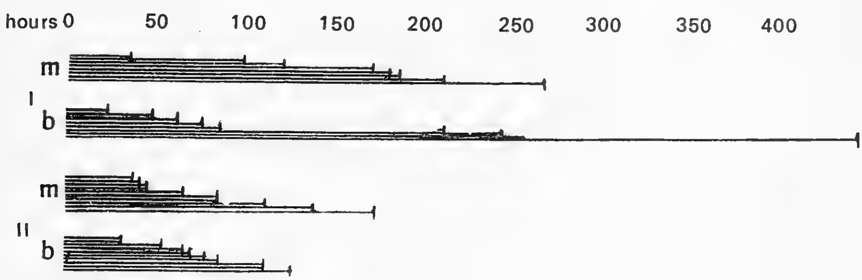


Diagram 45. Resistance to desiccation. Experiments 140, 142, p. 108.
I—*Calathus mollis*; II—*Bradycellus collaris*. m—Macropterous form; b—Brachypterous form.

*Of the 20 specimens used in the experiment 11 died.

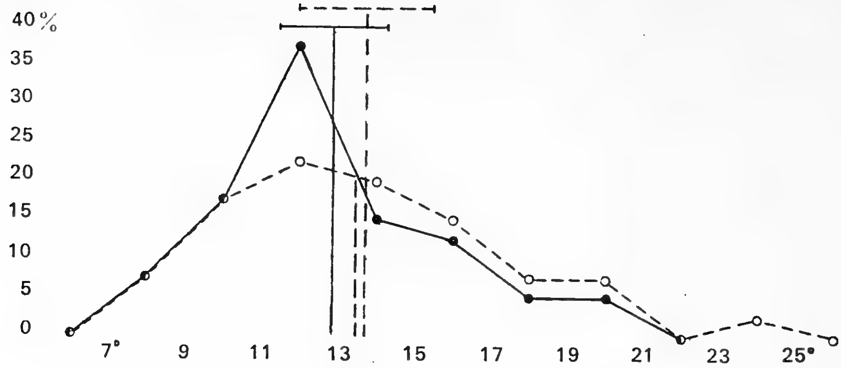


Diagram 46. *Bradycellus collaris*, macropterous form (continuous lines); brachypterous form (broken lines). Frequency curves for temperature preferenda. Experiment 7, p. 70.

Vertical lines indicate arithmetic and statistical mean values (in macropterous form coinciding), horizontal lines represent calculated amplitudes of variation of the latter.

macropterous form 82.6 hours; brachypterous form 75.6 hours.

d. *Longevity under optimal conditions.* Fourteen specimens each of the two forms were put in a glass jar with branches and "förna" of *Calluna*. The contents were kept moderately moist at room temperature. The animals were fed on breadcrumbs. During three months (September 23 through December 23, 1947) altogether 5 specimens died, of which 3 were macropterous and 2 brachypterous. The culture was then destroyed by mistake.

These experiments apparently used far too little material. Hence they cannot support definitive conclusions on the selection value of the macropterous or the brachypterous form of dimorphic species on account of higher "general vitality." For, as discussed below (p. 365), even positive selective features, which in the long run cause significant differences in the composition of a population, may show such slight effectiveness in one generation that they can be experimentally established with certainty only with very large material (> 1,000 readings).

Nevertheless it is striking that of the 9 series of experiments carried out, only 2 (*Bradycellus collaris*, b and d) suggested a somewhat lower resistance
360 capacity of the macropterous form. The other experiments indicated the opposite. However, the difference in all cases is so insignificant that it lies well within the limits of statistically possible variation, and we may assume that—apart from flight capacity—there are *no* demonstrable physiological differences between the two forms of the species investigated (and probably among carabids in general). In any case we are not justified, as explained

below, nor is it necessary, to posit a general higher selection value of the brachypterous form, as Darlington does (1943).

I will mention two other phenomena which in my view contradict the idea that the brachypterous form of the dimorphic carabids generally has to show higher vitality than the macropterous form.

Such a selective advantage for the brachypterous form would be particularly significant at the periphery of the area, as in cases where the species in question has attained its existence limits. In an area of distribution stabilized in this way it could be expected that an outer zone of predominantly brachypterous forms would develop (but not of a "purely" brachypterous stock, since most individuals are heterozygous). However, no such situation can be demonstrated in the Fennoscandian fauna, and I doubt if the only reason is the short duration of the postglacial period. The apparent exceptions in the form of more or less "purely" brachypterous subareas in northern Finland and, particularly, in western Norway, are due to very different causes (the history of immigration), which are discussed below in detail. In northern Sweden such a phenomenon is demonstrable only where the stock represents a direct offshoot of the Finnish or of the Norwegian area.

An interesting special case is that of *Notiophilus biguttatus*. It is almost universally distributed in Fennoscandia, and in southern Scandinavia certainly represents one of the earliest immigrants, which has had long enough time in the area to achieve an equilibrium between the two forms by selection. Yet in southern Sweden, unlike most other dimorphic species, the macropterous forms are even in a majority (see p. 408). The reason seems clear: since the species is an eurytopic forest inhabitant the danger of elimination of macropterous forms that stray away in flight is small, i.e. selection does not
361 work against the flight capacity. A possibly existing advantage of vitality in the brachypterous form would have caused such a selection—which did not happen!

2. *Selective importance of flight capacity.* In its simplest form this factor was cited by Darwin (1859, pp. 135–136) when he set out to explain the richness of flightless Coleoptera on Madeira. He believed the flying forms were gradually swept out to sea by the wind. Darlington (1943) is certainly correct when he argues that the situation is not so simple. Exposure to the wind, namely, is not decisive; in the southern Appalachians as well as in the Greater Antilles totally wooded mountains are also characterized by the same high number of flightless carabids.

Darlington tried to explain the significance of flight capacity on a purely ecological basis (p. 58): "The principal function of flight among geophile Carabidae is found to be to maintain sparse, unstable populations in large, unstable areas†." He mentions a few examples of such "unstable" biotopes (also in his

†(Original quotation in English; area = region; suppl. scient. edit.)

work of 1936, pp. 156 ff.). For the Fennoscandian Region the following ecological groups have to be taken into consideration:

First, the *ripicolous* species. "Shores in general may be the most unstable of all biotopes[†]" (Lindroth, 1943a, p. 126). In our region there is no constantly brachypterous carabid that is strictly ripicolous in this sense, with the characteristic exception of the two species, *Aëpus marinus* and *Trechus fulvus* confined to the seashore, and *Elaphrus angusticollis* in eastern Fennoscandia. Nevertheless, *Agonum moestum*, *Bembidion assimile*, *B. schüppeli* and *B. transparens* are dimorphic, as also *Carabus clathratus*; also dimorphic are the less strictly ripicolous species *Bembidion clarki*, *B. gilvipes*, *B. guttula*, *Dromius sigma* and *Pterostichus anthracinus*.

Second, the species of *open* terrain, in the large high boreal forest regions, where only small, often variable patches are available. It is quite characteristic that in the most undisturbed forests of Fennoscandia, such as those of eastern Karelia, such dimorphic species as *Amara infima*, *Bradycellus collaris*, and *Pterostichus strenuus* are found predominantly in their macropterous form.

Third, the species of *cultivated soils*. The farther north, that is the more recent the cultivation and the more predominant the macropterous carabids on cultivated soils. North of latitude 64°N there are absolutely no brachypterous
362 species associated with cultivation or even favored by cultivation. The exceptions are just two solitary records of *Pterostichus vulgaris* (possibly resulting from passive dispersal), in addition to *Bembidion lampros*, which in the north is slightly favored by cultivation.

"In small, stable areas (= regions)[††] where populations are dense and stable, flight presumably loses this function" (Darlington, l.c.; cf. quoted above). Such biotopes occur in Fennoscandia mostly on the seashore and in high regions of the fjelds, both of which have at least a *relative* stability. Much more pronounced ones are found outside our regions on *old* islands and (from the biological viewpoint) *old* montane regions. It is strange, however, that Darlington on the one hand ascribes a great positive role to the flight capacity for those species that are able to protect themselves in this way against alterations in the biotope, on the other hand he does not concede the corresponding *negative* role to the same characteristic for "stable" species. He repeatedly emphasizes that for these species the flight capacity is "useless, but not necessarily harmful." I find this illogical. The flight of all or some individuals of a given population signifies rapid dispersal or thinning out over a larger region*. If thereby new habitable land is colonized the result is positive (from

†(Original German quotation translated into English; suppl. scient. edit.).

††(suppl. scient. edit.).

*Concerning the flight capacity of carabids and its ecological significance, see a later section (pp. 573 ff.).

the viewpoint of preservation of the species), especially if the original habitat has changed in a disadvantageous direction. But if the emigrants get an unsuitable region they are destroyed without producing progeny and this must happen the oftener, the smaller and more isolated are the regions habitable by these populations.

Concrete examples are provided by the drift material of insects, especially at the south coast of Finland (see also *Bembidion gilvipes* and *B. lampros* in Part I). Palmén (1944) assumed with reason that they originated predominantly from Estonia. The occasional occurrence of a larger number of dimorphic species* in the drift material *exclusively in macropterous form* must signify a
363 considerable impoverishment thereof in the original populations in Estonia, without any conceivable corresponding influx of immigrants to the regions of population. *Selection has taken place in favor of the brachypterous form.* The same is true of the frequent "stragglers" of dimorphic species of the plains, also observed by Darlington (for instance, 1943, pp. 59–60) on the "Presidential Range" (New Hampshire) in the *regio alpina*, where they must die with no possibility of reproducing.

Finally the maps on the distribution of the two forms of a number of carabids, discussed in greater detail below, show that selection actually takes place, which at least in part depends on the flight capacity of the macropterous forms.

Attention may also be drawn to an experiment with *Drosophila* which, however, was somewhat too simple (l'-Héritier, Neefs and Teissier, 1937). A mixed population of "wild" and "vestigial" types was exposed to a moderate wind in the open over a long period of time and was continually studied statistically. The experiment showed the not unexpected result, that the component of *vg* in the population gradually increased.

Darlington's reluctance to accept Darwin's old concept**, even with reservations, is evidently due to the fact that he thought more of passive wind transport ("blown out to sea": Darwin, l.c.) than on the active flight of insects. He claims wind exposure for those localities where the brachypterous forms are in a majority, to support Darwin's hypothesis.

However, the voluntary flight of the animal is the essential precondition, and a selection in favor of brachypterism may take place equally well in protected (for example, wooded) places, provided *the habitable areas* (for example, a certain region of altitude in the mountains) *are sufficiently small and isolated.*

*The dimorphic carabids of the Finnish drift material (Palmén, 1944) are: *Agonum fuliginosum, A. moestum, A. obscurum, Bembidion assimile, B. gilvipes, B. grapei, B. guttula, B. lampros, B. schüppeli, B. transparens, Bradycellus collaris, Calathus erratus, C. melanocephalus, Metabletus truncatellus, Notiophilus aquaticus, N. biguttatus, N. palustris, Pterostichus diligens, P. minor, P. strenuus, P. vernalis, Trechus rivularis.*

**Darlington (1943, p. 58) states: "Facts here given contradict the old Darwinian idea that insects on mountains and islands are flightless, with atrophied wings, because flying forms are blown or straggle away from exposed environments."

Probably anabatic mountain winds (anabatic valley winds; Geiger, 1942, p. 236) in the afternoon have an important role in transporting "stragglers" to higher, unfamiliar areas. A good example is provided by the frequent mass occurrence of woodland insects in snowfields of Fennoscandian mountains.

The only situation where selection in an isolated population of dimorphs would *not* affect the macropterous form would be where this form does not
364 fly. Nevertheless, the above list (Table 27, p. 377) shows that 25 of the 67 European dimorphic species have been observed flying, and this feature could apply to the macropterous form of all species.

I regard as confirmation of the above exposition the fact that among the dimorphic species widely distributed in our region the macropterous form has been maintained the longest—also in regions colonized early in the post-glacial period—in such species that are markedly *eurytopic* (examples: *Bembidion lampros*, *Bradycellus collaris*, *Calathus erratus*, *Notiophilus aquaticus*) or live in extensive and continuous biotopes (forest species: for instance, *Notiophilus biguttatus*, see p. 360; eurytopic hygrophilous species: *Bembidion guttula*, *Pterostichus minor*, *P. vernalis*), apparently because in such cases the macropterous migrants do not perish so often. On the other hand, in the case of *stenotopic* species with limited possibilities of colonization, selection sooner favors brachypterism. Examples are: shore species (on the seashore and larger lakes), such as *Bembidion assimile* and *B. schüppeli*; and xerophilous species, such as *Amara infima*, *Bembidion nigricorne*, *Cymindis macularis*, *Dromius linearis*, *Pterostichus lepidus*. But there are many exceptions to this rule, due not to present but to past conditions of the environment. These are considered below.

Stability, *area restriction*, and *isolation* of the biotopes favor *brachypterous* species and forms. Variability, extension, and moderate splitting up of biotopes favor macropterous species and forms. From this it follows that *in periods of alternating stability and variability—above all with respect to the climate—species with wing dimorphism are favored. This is applicable for the Quarternary period with its alternating glacial and interglacial epochs.* Hence Darlington and I came to the same final conclusion; our conception differs only with regard to the way selection operated.

Since the development of wing dimorphic species in the Fennoscandian region now apparently opposes any increase in the brachypterous form, it would be interesting to study the purely theoretical calculations, that have been made on the effect of selection in closed† populations. Perhaps in this way an idea of the length of time required can be achieved. Such calculations were undertaken by Haldane (1932, p. 184), in part cited in Huxley, 1942, p. 56 etc.

365 A pertinent case in this connection is selection in favor of a dominant gene located in an autosome. Other factors (recurrent mutation, chance) are here ignored. The assumed selective value is very low, 0.001. That is, the ratio

†(in the sense of "isolated"; suppl. scient. edit.).

between the phenotypic dominants and phenotypic recessive increases from 1 to 1.001 per generation. In the carabids (with very few exceptions) one generation can be equated with one year. Increase of the favored dominant takes place at the following rate:

Population increase from 0.001 to 1% in 6,920 generations.
Population increase from 1 to 50% in 4,819 generations.
Population increase from 50 to 99% in 11,664 generations.
Population increase from 99 to 99.999% in 309,780 generations.

If the selective value of the dominant is higher, the process will be that much quicker in the beginning. But the ominous last one percent is not completely eliminated even with *total* selection of the recessive. The latter can affect only the homozygotes, since only these express the recessive gene phenotypically. Even in the extreme case where these homozygotes constitute only 0.001% of the individuals of a population, not less than 0.2% of the dominants are heterozygotes (Haldane, 1932, p. 185).

Applying these considerations to mankind one came to the conclusion that sterilization of the recessive homozygotes with one or other hereditary defect is successful only where the gene in question occurs fairly frequently, as perhaps in hereditary imbecility.

It is evident from these calculations that even a selection that operates lightly brings about a fairly rapid increase in the favored mutants up to 99%, but the last one percent can never completely disappear by selection alone if this mutant is dominant. This is the problem of Achilles and the tortoise: an unending series of gradually decreasing numbers. —However, if a population is small and remains isolated over a long period of time the inferior form is finally eliminated by *chance*. If we imagine a population normally with 100 individuals on an average in which the gene for the recessive character with low selection value is present in only 1%, thus on an average present in one individual at any time (heterozygotic), then it might happen in the course of generations that as a result of this or that mishap—i.e. by
366 chance—this heterozygote one day fails to develop or find an opportunity to reproduce.

In the case in question, where the inferior factor represents a recessive gene, it is naturally impossible to decide whether this gene has completely disappeared or not in a given population, be it experimentally or by observation in nature. In mammals and other larger animals it is perhaps practicable to verify the existence of the recessive gene by active crossing of all individuals of the population (with the recessive homozygotes). In insects this is simply not possible since we cannot track down all the individuals of even smallest populations in nature. Remainders of "the macropterous gene" are even certain in many carabid species, that we today consider (rightly, from the phenotypic point of view) "constantly short-winged." However, similar cases where the rare accidental pairing of two heterozygotes has resulted in solitary

macropterous individuals (for example, in *Dromius sigma*, *Notiophilus germinyi*, *N. reitteri*, of which only one macropterous individual is known in each case), have provided occasion for use of the dubious term "atavism" ("regressive form," Kolbe, 1920, p. 393).

All brachypterous and apterous species of Coleoptera have undoubtedly arisen secondarily (cf., on the contrary, Horn, 1907). The study of species with wing dimorphism reveals the evolutionary path taken: *mutation*, *selection and chance**. Species whose wings are particularly heavily reduced, have perhaps been affected by more than *one* mutation. Because of this, and perhaps due to the markedly favorable effects of the wing-reducing mutation on the general vitality of the insect, certain species can achieve a condition of genetically "pure" brachypterism more rapidly than others. However, the main precondition might have been temporary isolation in small populations.

Distribution of Dimorphic Forms

The geographical distribution of the two forms of a wing-dimorphic species
367 of insect has been little studied. J. Sahlberg (1868) and Håk. Lindberg (1929) give a very general statement that brachypterous Hemiptera in the north and in the outermost parts of the Skärgård of southern Finland (Lindberg) are more frequent. With regard to *Gerris asper* L., Ekblom (1941, p. 61) denies this. Darlington (1938) attempted to map the three North American species of *Patrobus*. I have published (Lindroth, 1939) preliminary dimorphic maps of *Calathus mollis*, *Bembidion transparens*, and *B. aeneum*.

In the zoogeographical context, as in the present contribution, the chief concern is to map the dimorphic species and to explain the results. For species whose macropterous form is extremely rare a map would be superfluous. For other species sufficient material was not available or the distribution of the two forms did not appear to support any conclusions. Nevertheless, of the 50 dimorphic carabids occurring in Fennoscandia exactly one-half were found to be of zoogeographical interest in one way or another, and for this reason 25 dimorphic maps are provided in the present account.

Before I discuss the individual maps a few remarks on their method of notation might be in order. Each locality (or complex of localities located close together) is indicated by a circle whose size** is proportional to the number

*I cannot consider Reinig's (1938) "*elimination*" as a factor comparable with the three mentioned above. It is a result of chance, to a certain extent reminding one of Sewall Wright's "*drift effect*" (for instance, 1931, p. 147, Fig. 18; 1932; see also Huxley, 1942, p. 58 and elsewhere). Moreover, the term chosen is unfortunate since what is involved is not actual elimination (= destruction) but a sifting out and uneven distribution of the genotypes throughout the total area of a species.

**The relative size is easily underestimated. The largest circle of *Bembidion grapei* (38 Alta), for instance, corresponds to 80 individuals (Fig. 50).

of individuals examined*. It must be borne in mind that an aggregation of large circles does not necessarily signify a "focal point" of the area, but rather a well-explored region. However, the larger the circle, the more reliable in general** is the picture it provides of the actual distribution of macropterous and brachypterous forms. Distribution of *macropterous* individuals is shown by blank circles or blank sectors, of *brachypterous* individuals (intermediate specimens are also included) by *black* circles or sectors.

The reliability of a dimorphic map is completely dependent on the amount and versatility of the material studied. However, it is almost always impossible to obtain voucher specimens of a species from all the Fennoscandian localities
369 for study. In some cases this is to be lamented, in most other cases the gaps were more or less filled with nearby localities. To avoid unnecessary confusion, localities that have not been taken into account have generally been left out of the distribution maps; in a few cases they have been marked with crosses. Comparison with the general distribution maps in Part II of this work allows at least a judgement on the completeness of the dimorphic forms.

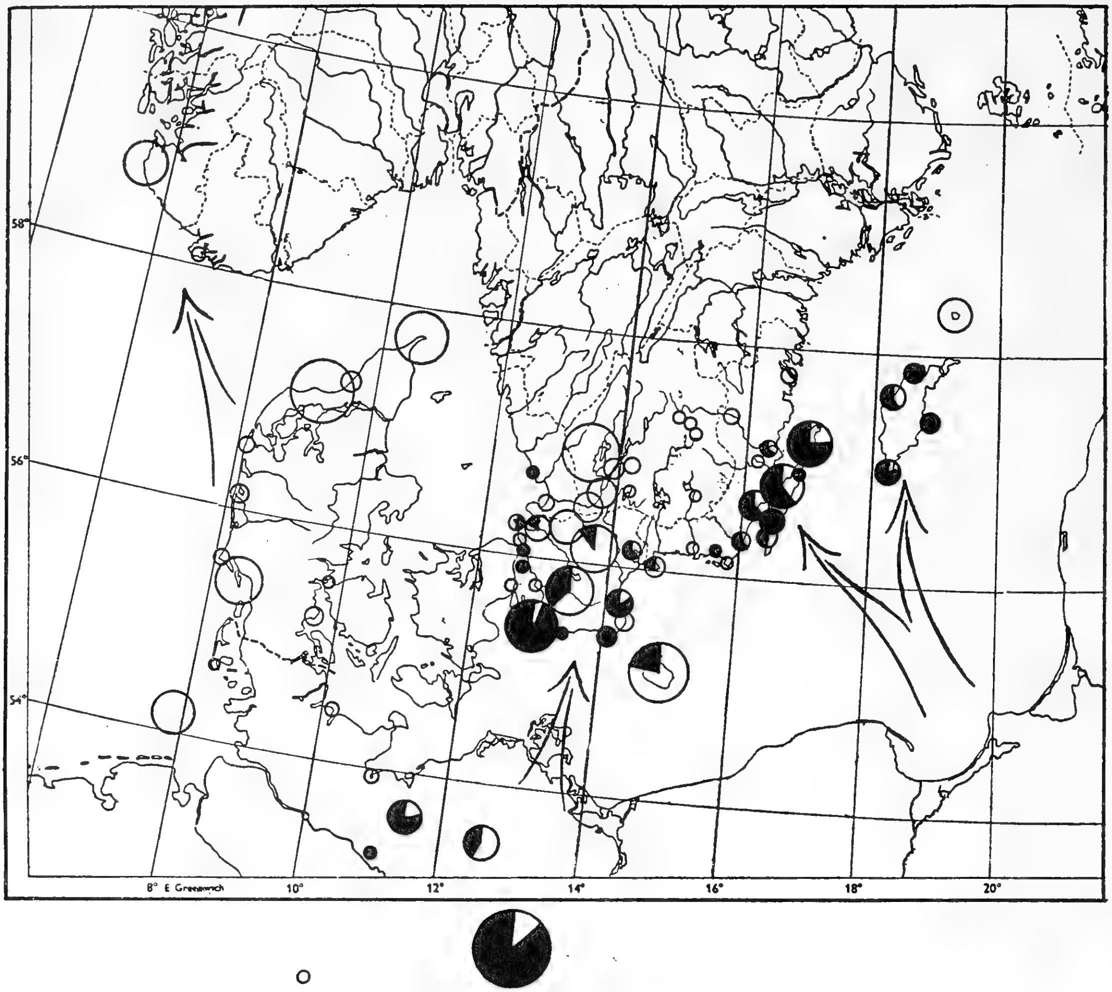
The arrows in some of the maps mark the more or less established postglacial migration route. Occasionally areas populated predominantly or exclusively by brachypterous forms are demarcated with special lines. For these and other indications see key with each map.

It is advisable to begin with *Calathus mollis* (Fig. 28, cf. also Fig. 25). The distribution in Sweden distinctly illustrates the principle that is more or less clearly valid for most of dimorphic species (originally probably for all): *At the periphery of the area of distribution* (in this case in the north, particularly inland) *there are predominantly or exclusively macropterous specimens*; *a preponderance of brachypterous specimens is found in regions colonized early.* According to the modern "invasion terminology" it may be said that the macropterous forms represent the "parachutists," the first to come in by air, whereas the brachypterous form is the soil-bound infantry, which has to march on its own. Since the macropterous form represents homozygotes, no brachypterous specimens can result from their pairing (unless a wing-reducing mutation recurs); on the other hand the brachypterous stock more or less comprises heterozygotes, from which macropterous specimens can be produced.

In extensive material from western Denmark and Norway (respectively 95 and 19 specimens), not a single brachypterous specimen was found. Apparently an isolated, genetically pure macropterous stock with a western distribution predominates, for instance, in West Germany and in the British Isles. It can also be separated by insignificant morphological characters (including those of the parameres of the male) from the Swedish form ("f. *typica*"; see Sup-

*Only the map of *Bradycellus collaris* (Fig. 48) is not quantitative.

**Exceptions are mass catches of wind-driven individuals, which are exclusively macropterous. For instance, see northern Öland in the map of *Bembidion lampros* (Fig. 40).



368 Fig. 28. *Calathus mollis.*

Distribution of wing-dimorphic forms. Blank circles and sectors: Macropterous specimens. *Black* circles and sectors: Brachypterous specimens.

The area of circles is proportional to the number of individuals examined. Two circles outside the map indicate Braunschweig (one specimen) and Berlin (53 specimens).

plement). Both forms occur together only on Bornholm, but there only the eastern one ("subspecies *erythroderus*") is dimorphic.

The species undoubtedly reached Norway by flying across the sea from Jutland (or from the old "Doggerland"), but Sweden was *not* reached via Denmark. In Denmark (excluding Bornholm) just one *macropterous* specimen
370 of the eastern form was found near Copenhagen. Immigration to Sweden must have taken place directly from the south. Another noteworthy fact which now emerges is the strong preponderance of the brachypterous form not only in the southern Skåne but also on Öland and Gotland (to a lesser extent on Småland along the Kalmarsund strait), whereas in the intervening regions, on Småland and Blekinge, only the macropterous form occurs almost everywhere. Study of more material from the last-mentioned province would be highly desirable, but even if the percentage of the brachypterous form was found to be fairly high, we could not speak of a coherent, homogenous brachypterous stock in southeastern Sweden. Three hypotheses might explain the situation:

1. The environmental factors on Öland and Gotland operate in favor of a stronger selection of the brachypterous form (or even the emergence of recurrent mutations).

2. The desired homogeneous brachypterous stock (Skå—Ble—Öld—Gtl) actually existed earlier during a climatically more favorable period. With the worsening of climatic conditions, the species as a whole was pushed back toward the southeast coast and was restricted to two subareas perhaps due to a gap in Ble. Subsequent recolonization in the present comparatively favorable climate took place chiefly by the macropterous form.

3. Öland and Gotland obtained their *mollis* stock by separate immigration and *not* through Skåne.

The map shows that I consider the last of these the only acceptable hypothesis. Hypothesis 1 should also have to explain why selection (or mutation frequency) on Skåne has been stronger on the south than on the other coasts. Moreover, some of the following maps of the other species show that the operation of selection on Öland and Gotland generally does not favor the brachypterous form in general (for example, *Harpalus azureus*, *Bembidion assimile*, *B. obtusum*). The problem of the origin of recurrent wing mutations is considered later (p. 403).

There are more serious objections to hypothesis 2. Such a "pulsating" postglacial immigration, even with periodic retreats, is certainly true of most species. Such a hypothesis cannot be ruled out. However, the following fact strongly supports hypothesis 3: *Calathus mollis* reached Skåne and (partly)
371 Bornholm not via Denmark but directly from the German Baltic Sea coast (even in brachypterous form). It is difficult to see how this could have come about other than by direct land connection. Under such standard conditions in the southern Baltic Sea, if not a firm land connection, then a far more favorable situation must have existed between Öland–Gotland and the continent,

which made possible a direct immigration in that direction. This question has already been considered above in detail in the section on "The Fauna of the Islands" (pp. 306 ff.). It was clear that *Calathus mollis* is only one of numerous species on Öland–Gotland which on faunistic grounds indicate the mentioned land connection. To the north a counterpart of Gotland in Gotska Sandön, which has remained continuously isolated since its postglacial origin. *C. mollis* certainly reached there by flight; the 10 specimens studied are macropterous.

Harpalus picipennis and *H. neglectus* (Figs. 29, 30) provide interesting comparisons with *Calathus mollis* and are to some extent its counterparts. The former species was found in Skåne exclusively in macropterous form (13 specimens), whereas both forms occur on Öland. On the other hand *neglectus* is dimorphic on the Swedish mainland (Skå, Hll, Ble) with a preponderance of the brachypterous form, whereas on Öland of 26 specimens studied only 2 were brachypterous. The assumption that *picipennis* reached Öland via Skåne is improbable. On the contrary, a separate immigration to this island must have taken place, as assumed for *Calathus mollis*.

In some cases the morphic map provides very limited indication of the
372 history of the immigration of the species, valid only for part of the area. *Pterostichus anthracinus* may be mentioned as an example (Fig. 31). Its northern limit in Sweden, formed by the River Dalälven to the east, is apparently stable and relatively old, since it has been attained by both forms. But in the west (in Dlr and Vrm) only macropterous individuals have been recorded which apparently represent a later immigration. Four brachypterous specimens were

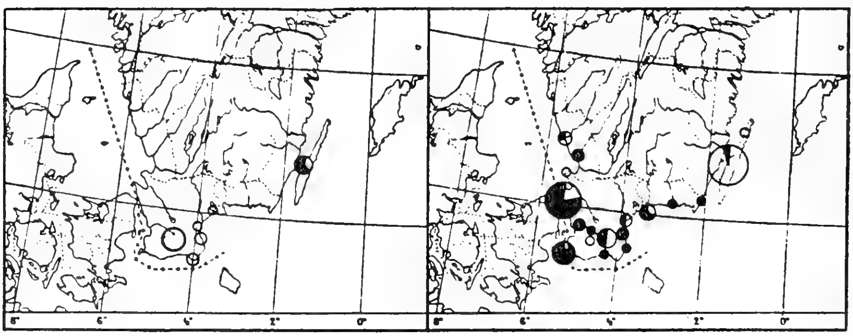


Fig. 29. *Harpalus picipennis*. Fig. 30. *Harpalus neglectus*.

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368).

found in Sv north of the mouth of the River Swir (outside the map), which is the only eastern Fennoscandian locality. Evidently this population did not arise from an accidental migration.

373 In the case of *Olisthopus rotundatus* (Fig. 32) both forms coexist almost throughout its area, with the noteworthy exception of the mainland of eastern Fennoscandia, where so far only macropterous individuals (altogether 18) have been collected, except for a single specimen from Ik Metsäpirtti (coll. LBG!)*. But on the main island of Åland the brachypterous form is already predominant (24 of 27 specimens studied), which conclusively supports the Swedish origin of this stock. For further remarks see the section on the Fauna of the Islands (pp. 239 ff.).

In *Amara infima* (Fig. 33) the macropterous form is rare. It has been recorded only in eastern Karelia as the only form occurring there (however only 3 specimens). Moreover, the brachypterous form has also been found in the northernmost isolated localities. These are thus no accidental migrants, which is of considerable interest in view of the discovery of this species only recently in Finland. The discontinuous distribution of the species probably reflects the concealed, almost subterranean mode of life of the animal.

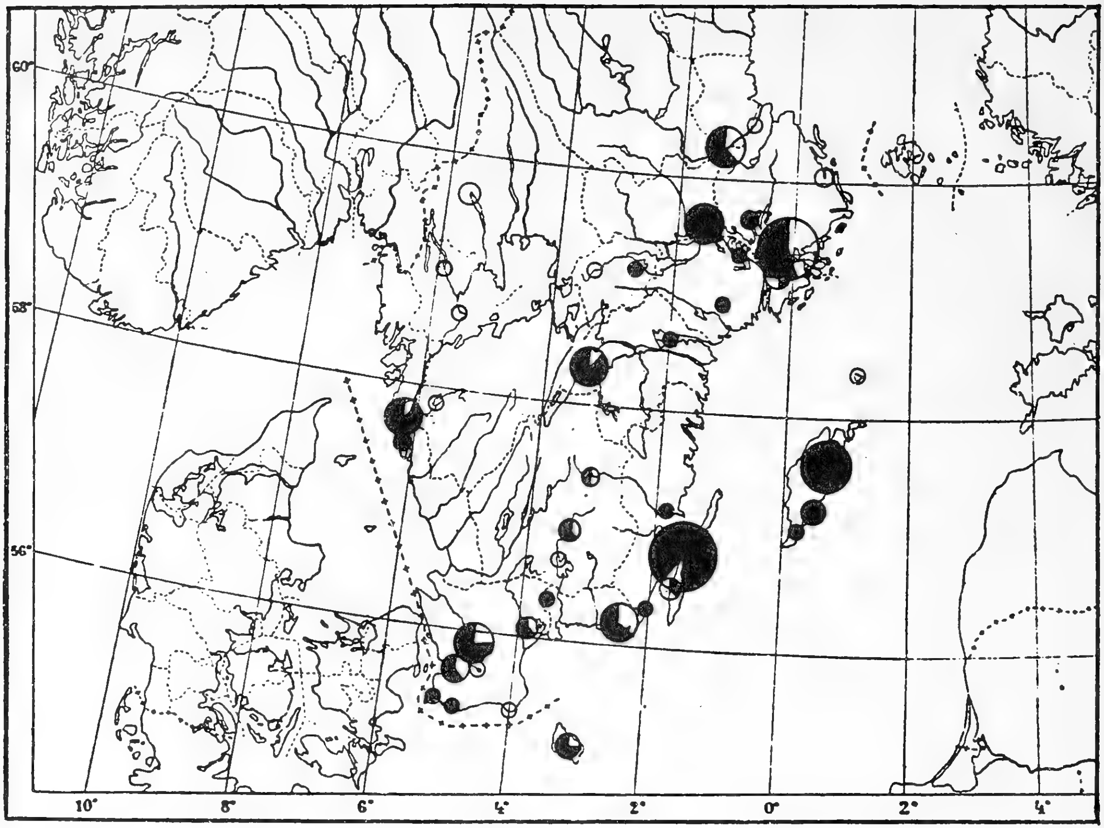
Harpalus azureus (Fig. 34) is the only example of a species that seems to occur on Öland exclusively in brachypterous form (86 specimens studied), but exists on Gotland in both forms. The distribution of the species there is not
375 completely irregular, but the macropterous form predominates, especially in the north, including Fårön, and also in the eastern part of the island. In the entire northern one-third, only one brachypterous specimen (Fårösund, JNS!) was found, as compared to 29 macropterous specimens. Apparently this part was colonized later. The problem is dealt with in more detail in the section on the Fauna of the Islands (p. 310).

377 The situation with regard to *Calathus erratus* (Fig. 35) is unusually clear. This species exemplifies the principles formulated and discussed for *C. mollis* on a large scale.

The hind wings of the macropterous form of *C. erratus* are weak and somewhat variable in size. Perhaps all the macropterous specimens (with the reflexed apical part of the wing) are capable of flight. However, they might be genetically uniform. That the markedly macropterous specimens have flight capacity is proven by the detection of this form only (64 specimens) in Finnish marine drift material (Palmén, 1944, p. 146).

In all three countries, north of latitude 62–63° N *C. erratus* occurs exclusively in macropterous form, whereas in the south, especially in Sweden, the brachypterous form predominates. It is quite clear from the map that the latter form has been able to advance in Norway along the Gudbrands valley

*One old brachypterous specimen (MH), bearing the label "Viborg. coll. Mannerheim," is better ignored.

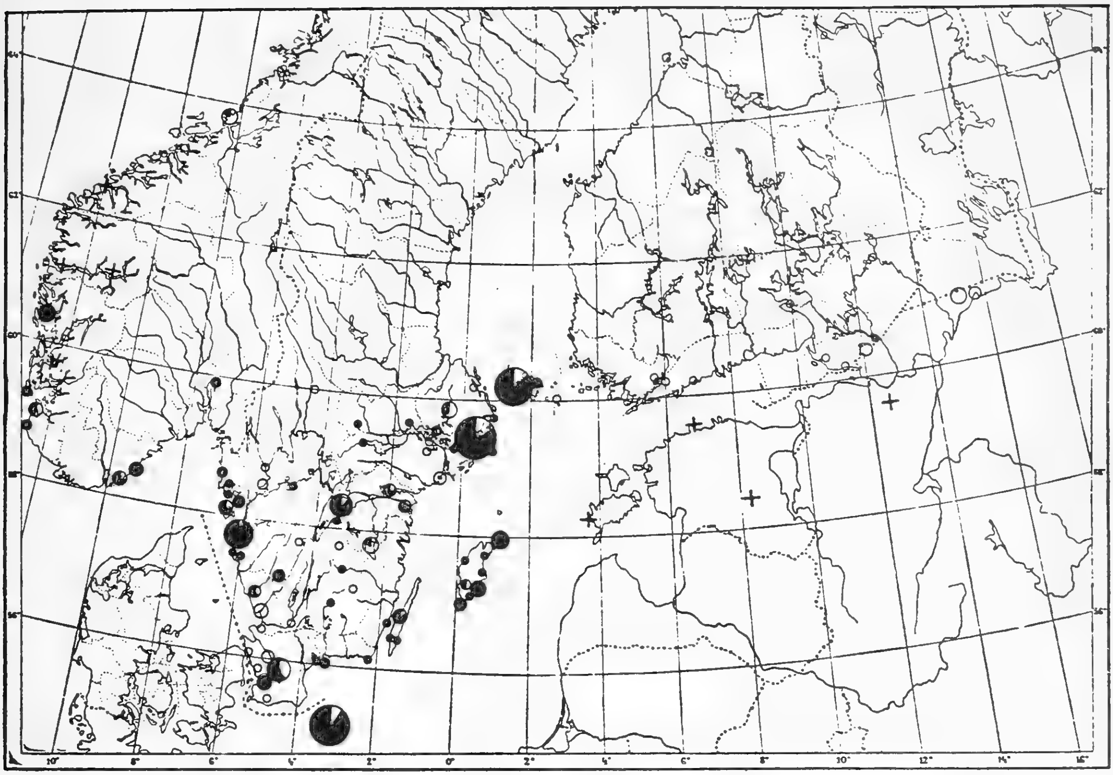


372 Fig. 31. *Pterostichus anthracinus.*

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Outside the map area, 4 brachypterous specimens were found at the mouth of River Swir in eastern Karelia.

almost up to latitude 62° N, but the *watershed toward the Atlantic seaboard* formed an effective barrier which could be crossed only by the macropterous forms. To the inner Sogn (Province 19), too, the species apparently came from the east by air. But in southwestern Norway (Provinces 4–6) exclusively the brachypterous form was found (26 specimens), which is evidence of an old colonization. In wooded areas, especially in central Finland and eastern Karelia, the macropterous form of this species associated with open terrain is conspicuously favored.

Noteworthy is the exclusive occurrence of the macropterous form in western Norway between latitudes 60° and 69° N. *Evidently external factors* (cli-

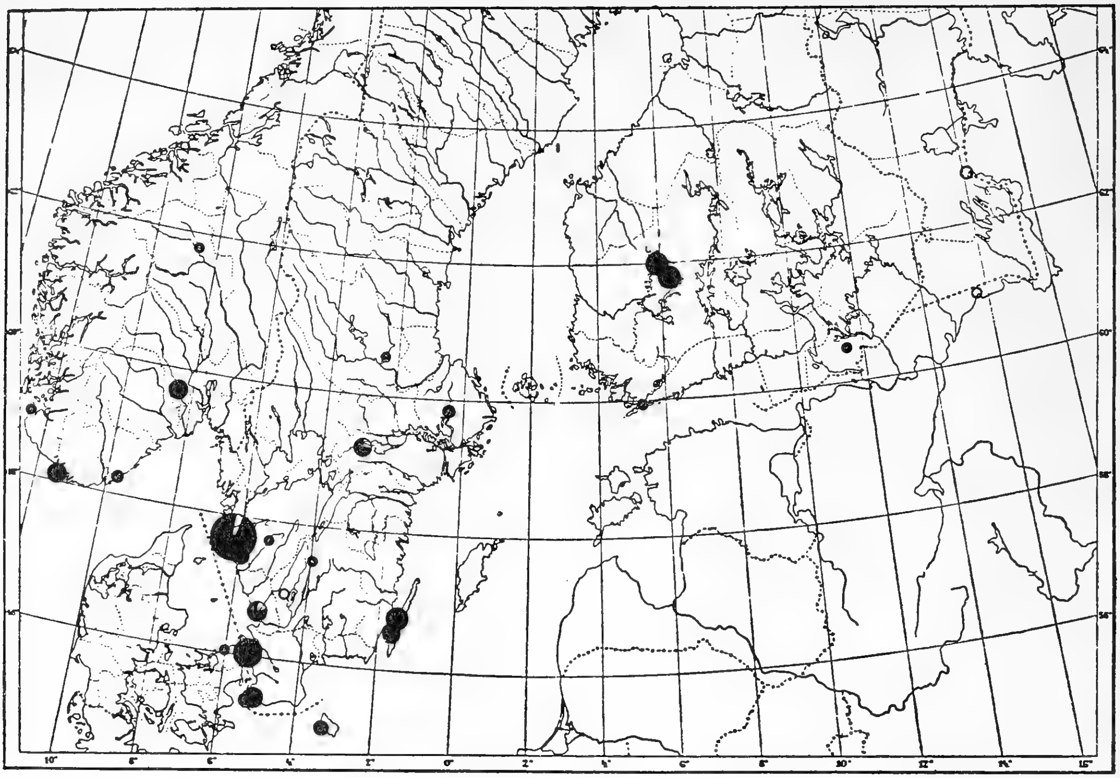


373 Fig. 32. *Olisthopus rotundatus.*

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Crosses indicate localities where no material was available.

matic or others) *are not alone responsible for the origin or advantage of the brachypterous form in western Scandinavia*. It is advisable to keep this fact in mind in the following treatment of other distribution types, which are nearly contrary to *Calathus erratus*.

The distribution of *Pterostichus vernalis* (Fig. 36) in the southern half of Scandinavia corresponds with that of *Calathus erratus*. The peripheral zone (northern and western), which is exclusively populated by the macropterous form, is less extensive. Unfortunately no reference specimens were available from 4 localities in western Norway north of Bergen, or from one locality in the upper Gudbrands valley, but with fair certainty they belong to the purely
378 macropterous zone. In contrast with *Calathus erratus*, *Pterostichus vernalis* is

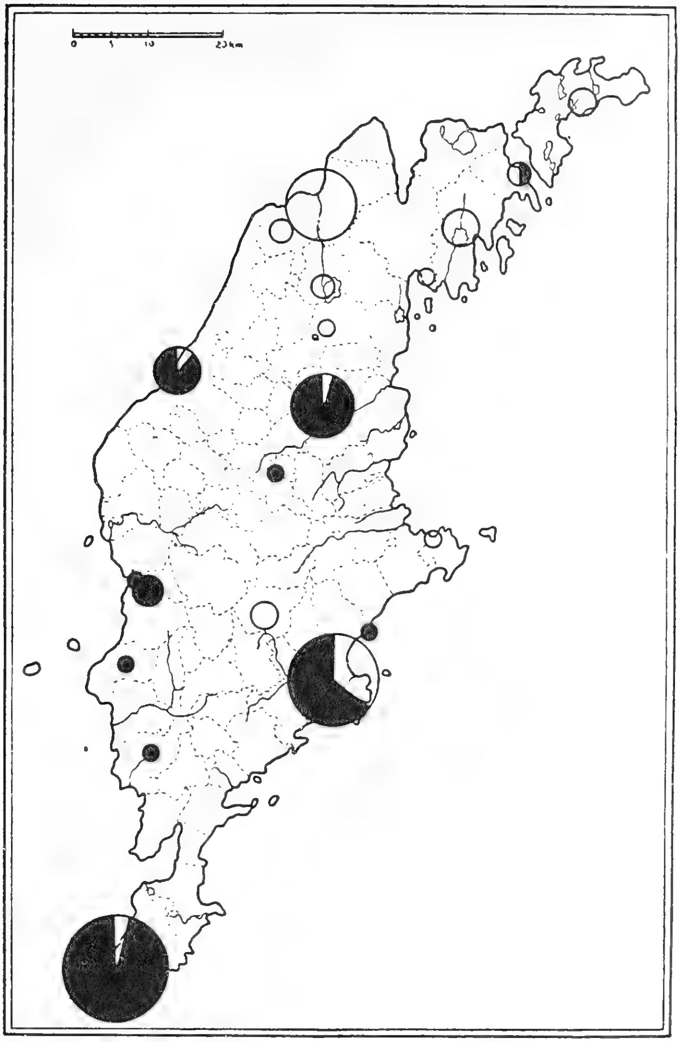


374 Fig. 33. *Amara infima.*

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368).

represented in southwestern Norway (Provinces 5–6) almost exclusively by the macropterous form, which appears to have immigrated there relatively late along the south coast.

Interesting conditions, differing from the aforementioned, are found in the Bothnian coastland, where the south Swedish stock extends only up to Mdp and is represented at this northern limit only by the macropterous form. But on the Finnish side along the entire coast the area is continuous, with its outermost point represented by one locality in Sweden (Nbt), which here
381 contains brachypterous individuals. This is strange, because a broad apparently "purely" macropterous zone seems to straddle central Finland. The possibility of brachypterism having arisen in the Bothnian coastland by late recurrent mutation cannot be denied. Or instead, the occurrence there is of relict nature.



375 Fig. 34. *Harpalus (Ophonus) azureus.*

Distribution of wing-dimorphic forms on Gotland. For explanation see p. 367 and Fig. 28 (p. 368).

The following species, *Pterostichus lepidus* (Fig. 37) and *Carabus clathratus* (Fig. 38), show a high degree of correspondence. Both occur in the south almost exclusively in brachypterous form: In Norway this is the only form recorded, in Sweden south of latitude 60°. N only 4 and 2 brachypterous individuals were found respectively (among 197 and 85 brachypterous speci-

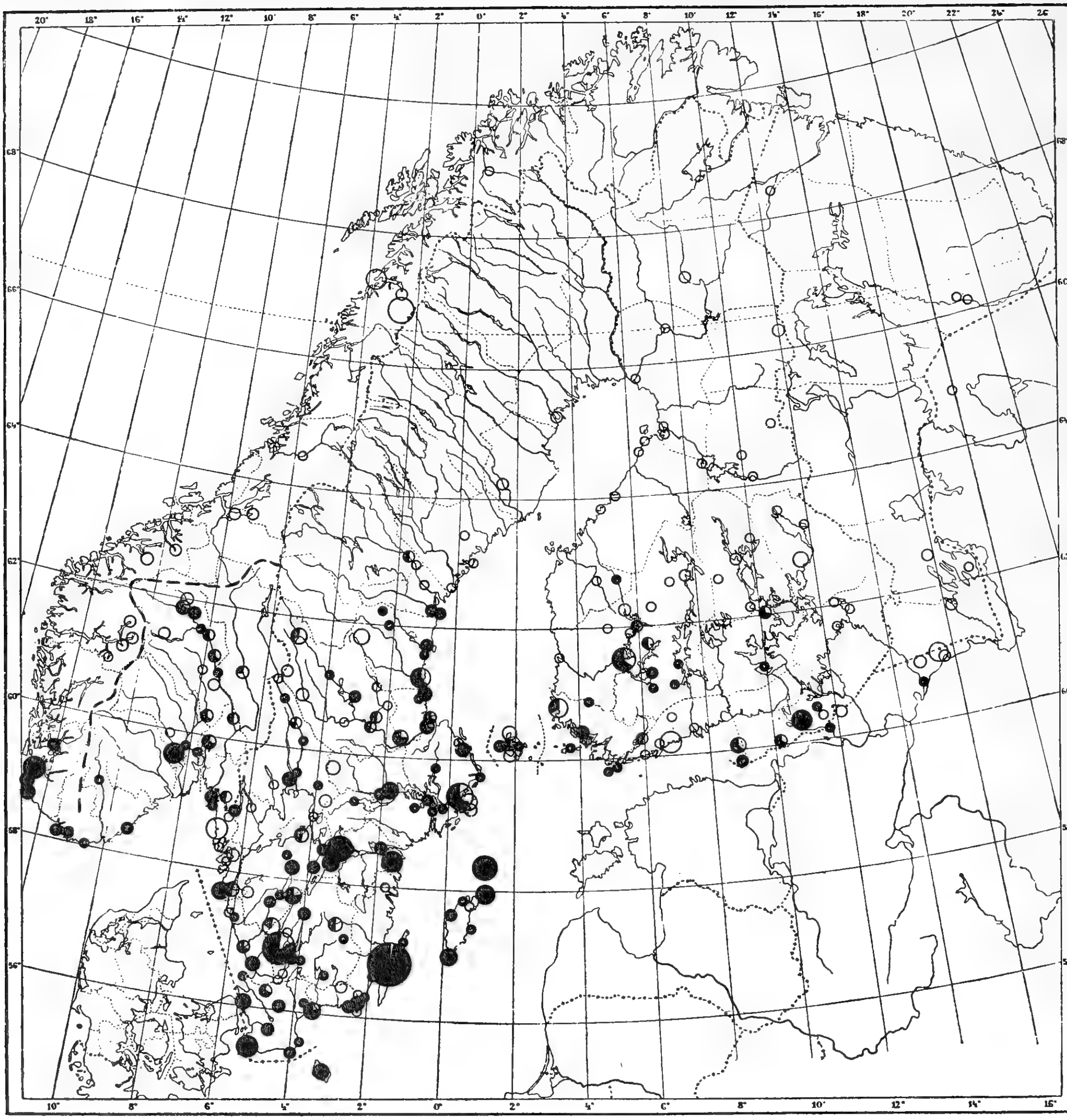
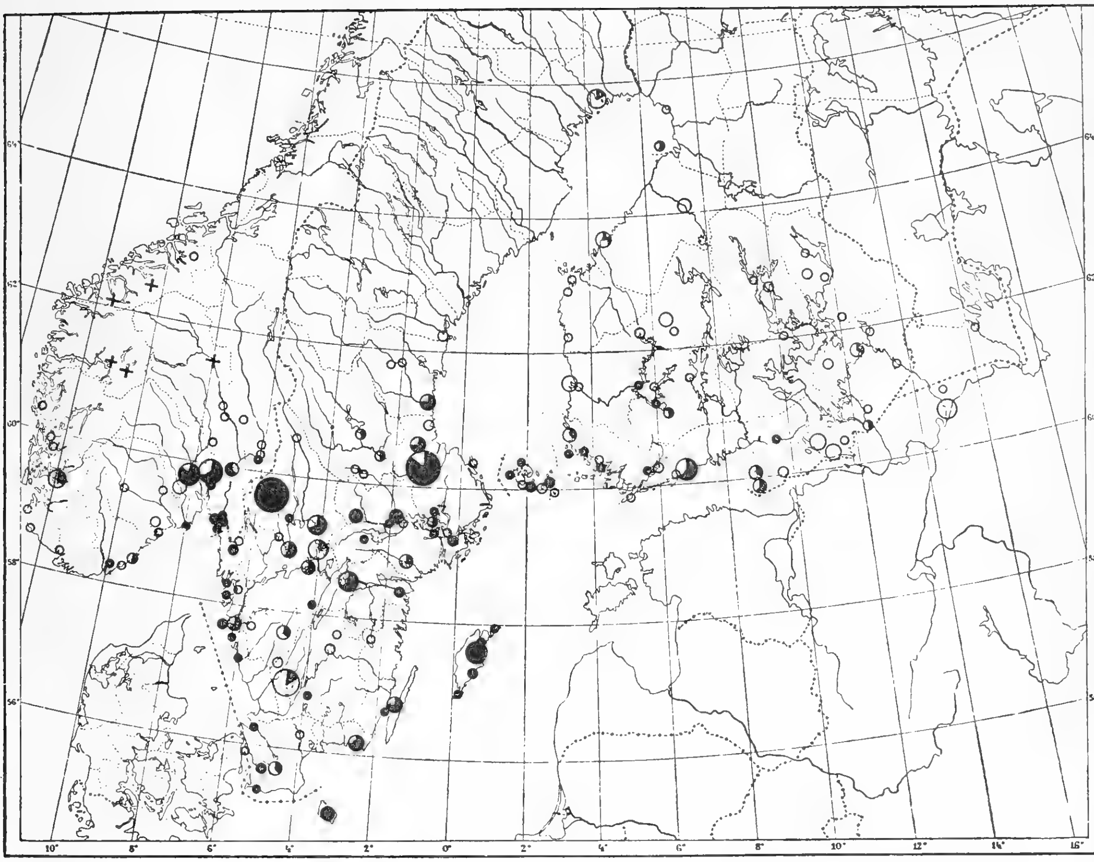


Fig. 35. *Calathus erratus.*
Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). In southern Norway the main watershed is indicated. Macropterous drift material from southern Finland (Palmén, 1944) has not been considered.



378 Fig. 36. *Pterostichus vernalis.*

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Crosses indicate localities where no material was available.

mens respectively); in Finland and east Karelia south of latitude 63°N several macropterous individuals of the *Carabus* species were found (5 among 27 brachypterous specimens). On the other hand only one macropterous individual of *P. lepidus* was found (among 96 specimens studied). No conclusions concerning immigration can be drawn from these parts of the area. But in the north, especially on the Swedish side, the macropterous form occurs more frequently. In the case of *P. lepidus*, on both sides of this "macropterous zone" the area is continuous, toward the southwest through Scandinavia and toward

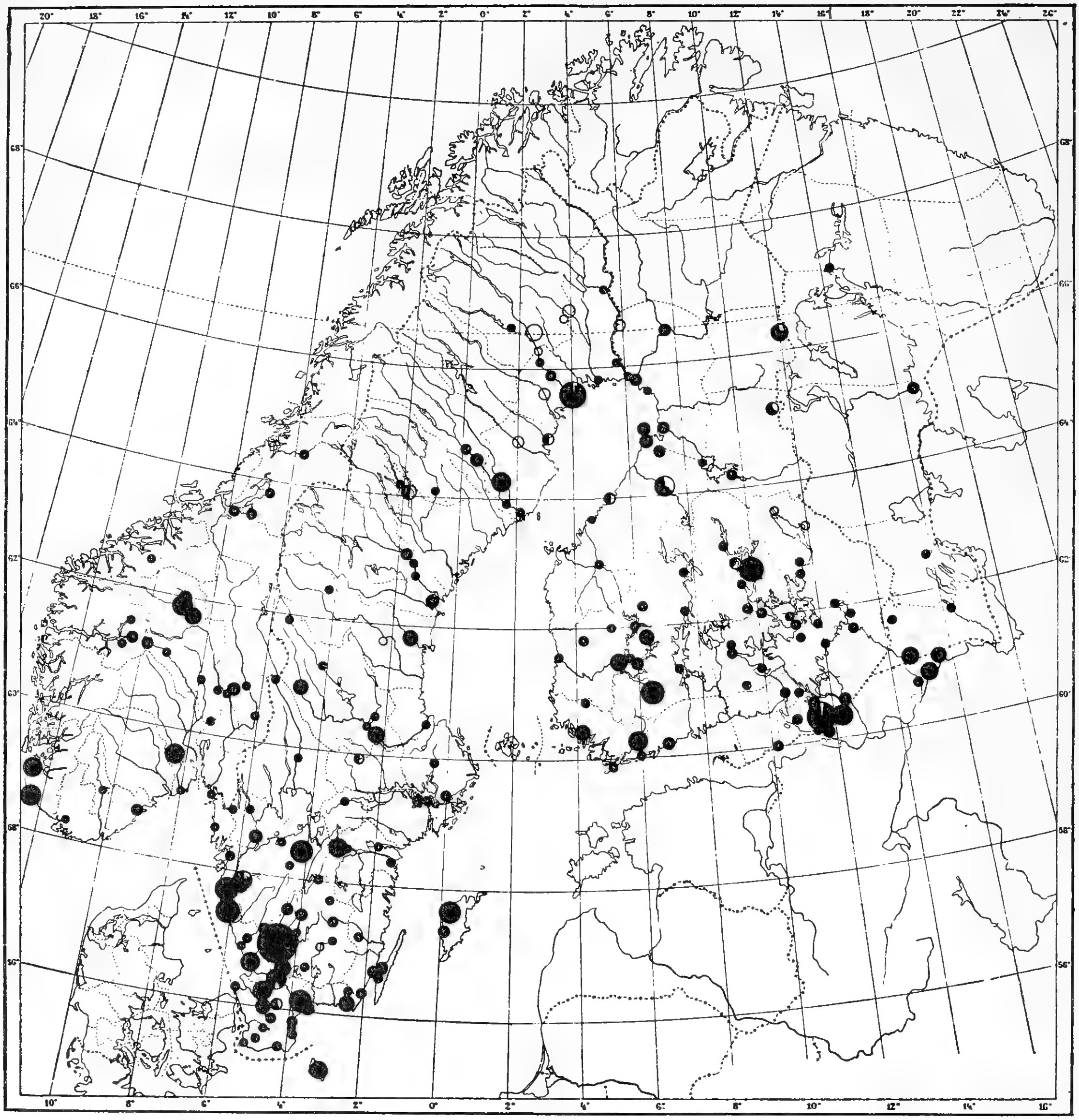


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Fig. 37. *Pterostichus lepidus.*

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368).

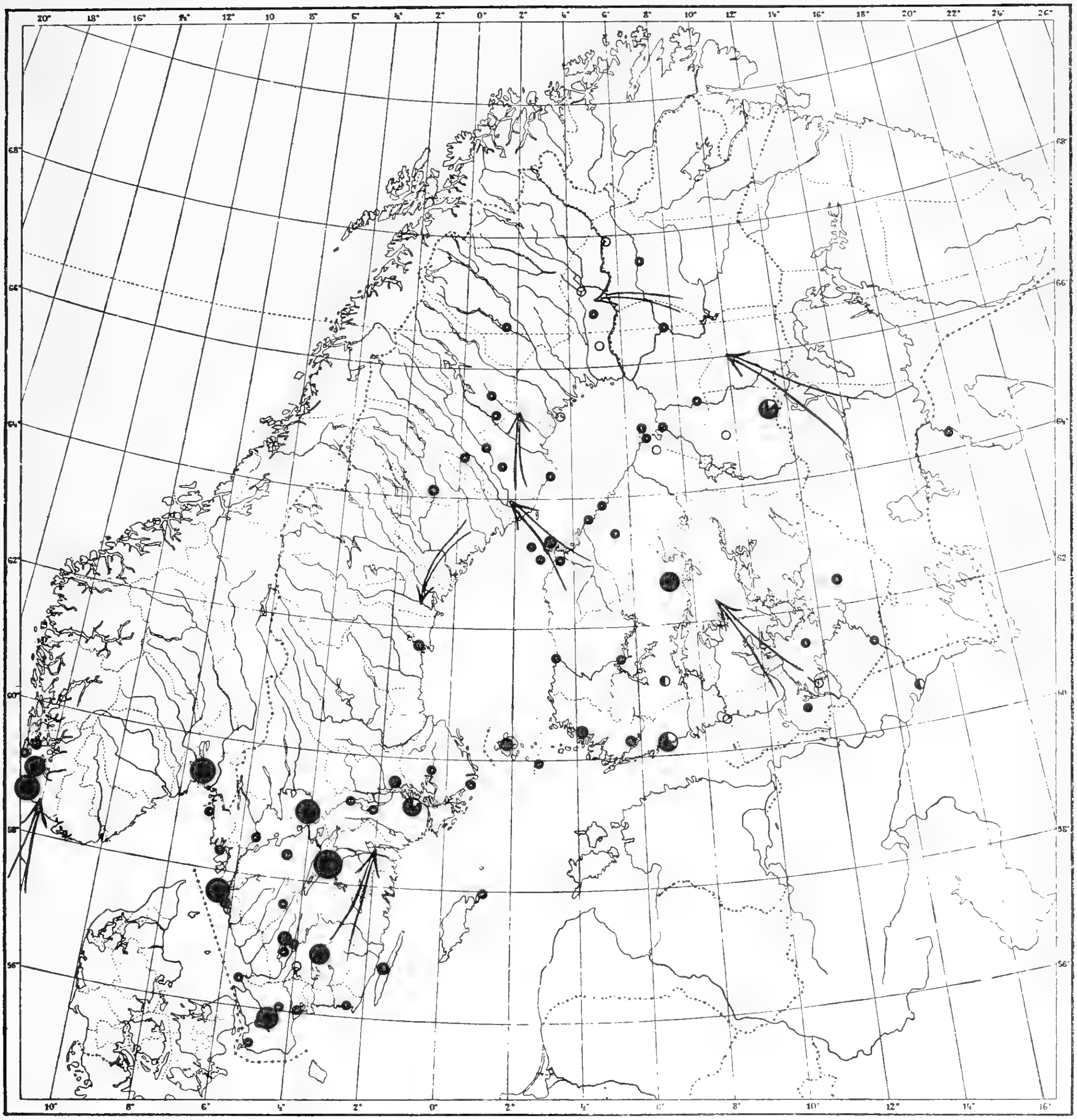


Fig. 38. *Carabus clathratus.*

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Arrows indicate possible routes of postglacial migration.

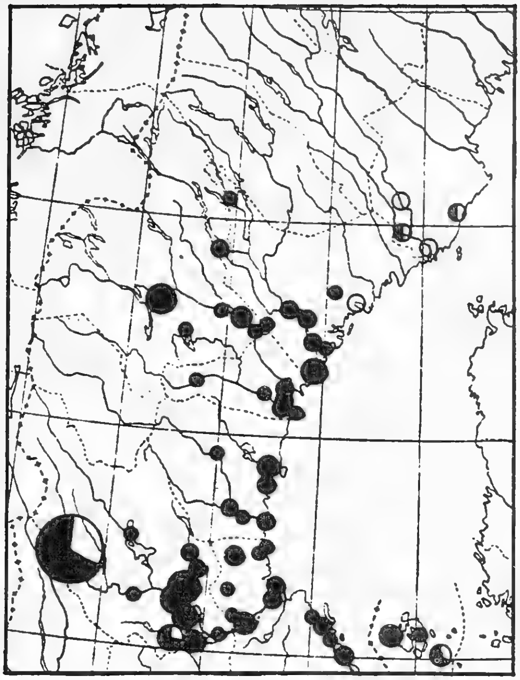
the southeast through Finland and east Karelia. We saw earlier that a high representation of the macropterous form indicates a recent colonization. We are consequently justified in seeing the zone of *P. lepidus* as the "scar," where the western and eastern stocks met and merged. It is characteristic that it lies on the Swedish side, which is not clearly evident from the usual distribution map.

Carabus clathratus actually differs only in one point, which is important: In Sweden south of the "scar" there is no detectable connection with the south Scandinavian stock. The old record in Hls is of course enigmatic, but may be connected with the northern subarea, because in northern Upl, in Dlr and Gst and in some regions that have been very well explored, this splendid species could hardly escape the collectors. I suggest we can understand the riddle better from the records on three small islands in Kvarken (the narrowest part of the Gulf of Bothnia). Probably the insect was successful in colonizing Sweden too by this route, in predominantly or (genetically) purely brachypterous form, so evidently by hydrochorous transport. The "scar" would then represent not the boundary between an eastern and a southern stock but
382 between two eastern stocks. In all probability, independent origin must also be ascribed to the isolated fairly numerous southwest Norwegian stock. This would mean that *Carabus clathratus* reached Scandinavia by 4 different routes.

The two species, *Pterostichus lepidus* and *Carabus clathratus*, show a further correspondence in a strip of macropterous specimens across central Finland (at about the height of Ule-träsk), which is most evident in the case of *Pterostichus* species. We find the same manifestation in the text below, especially in the case of *Pterostichus minor*. It is therefore quite possible that in this region too we have the last trace of a boundary between two originally separate immigrant stocks.

383 *Pterostichus vulgaris* (Fig. 39) represents a dimorphic species, whose macropterous form is extremely rare and is apparently continuously declining. From south Sweden (south of about latitude 62°20′ N), among hundreds of specimens so far collected, only 3 were macropterous (Skå Båstad; Boh Fjällbacka; Nke Hasselfors). As was to be expected, an exception is provided by the border zones, which could be checked only with Swedish material. There the macropterous form occurs somewhat more numerous partly along the boundary in the Province of Vbt and in northern Ång (8 macropterous, 3 brachypterous specimens) and partly in the localities that are highest and farthest from the coast in the parish of Lima in Dlr (10 macropterous, 23 brachypterous specimens). The last-mentioned material (Axel Olsson) was collected at irregular intervals over a period of almost 30 years. I tried to find out whether during this period a shift took place in Lima in favor of the brachypterous form. But I was unable to establish this, since the macropterous individuals were distributed fairly uniformly over the years.

It is particularly interesting that the macropterous form occurs at the



382 Fig. 39. *Pterostichus vulgaris.*

Distribution of wing-dimorphic forms in Sweden (and Åland) north of latitude 60°N. For explanation see p. 367 and Fig. 28 (p. 368).

northern limit *in the coastal region* but is unknown in the interior parts of Ång and Jtl. The former region was apparently colonized later, even though some inland localities (Jtl Ulriksfors, Ång Tåsjö) are at least equally far from the area of departure of the immigrating animal. This is a distinct example that river valleys are important migration routes in high boreal forest regions, where the intervening distances, which are partly forest, partly swamp, and only slightly cultivated, pose great difficulties especially to soil-bound animals of the open terrain, if they attempt to emigrate from one riparian region to another.

The dimorphic map of *Bembidion lampros* (Fig. 40), the most frequent and most eurytopic of our *Bembidion* species, has been worked out only for Sweden and north Finland. It provides no indications as to the immigration routes, since the brachypterous form, at least in Sweden (from north Finland too little material is available) has everywhere reached the outermost limits of the area. At first glance the picture appears to be completely uninteresting. But, this is not so. Actually such a map holds a very special interest, although

in a field that has not been touched on so far. What can be the significance of the fact that the brachypterous form has everywhere caught up with the macropterous one, in the north as well as in the mountains? Evidently, *that the species in question* under the prevailing conditions (climate, cultivation,
385 etc.), *has reached its existence limit* (existence-ecological limit). If not, if the species would still be in the state of expansion, then a border of leading "parachutists" should be expected. —The reader will perhaps ask whether in zoo- and phytogeography generally such existence limits are not taken into consideration, since isotherms, pH lines, occurrence of limestone, etc. are repeatedly used to explain the area of distribution. But the difference is that in most cases this is on the assumption only that the species concerned has achieved its existence limit, whereas in the case of *Bembidion lampros* we are justified in *asserting* that it has. It must therefore be of great general interest to map as precisely as possible the geographical limits of all such "stable" dimorphic species (provided that the macropterous form occurs more than as solitary individuals, which are inconsequential for dispersal biology), so we can determine the typical course of true existence limits, for instance, the northern limit within the Fennoscandian region. "Per analogia," we could then also distinguish between the existence and dynamic limits of species lacking wing dimorphism (details see below, p. 616).

387 Among the species considered earlier, the Swedish northern limit of *Pterostichus vulgaris* (Fig. 39) in particular, has the same stable type as that of *Bembidion lampros*. This is also true of *B. gilvipes* (Fig. 41), a species that occurs in all three countries in its brachypterous form up to the northern limit. Mapping was therefore limited to regions north of about latitude 60° N.

In *Bembidion guttula* (Fig. 42) we come across a new type in a way, where the geographical distribution of the macropterous and brachypterous form is not what might be expected. In the south, at least until latitude 62° N, the two forms are found intermixed; in one region the macropterous form and in another, somewhat more often, the brachypterous form predominates, but there is no extensive area where brachypterous specimens are found exclusively. The exception is found, strangely enough, in the far north, in Finland and in the Russian parts north of latitude 64°30′ N where solely the brachypterous form was found (altogether 11 localities, with 14 specimens). This population advances in Nbt also to the Swedish region, and characteristically shows macropterous specimens only at its outermost limit toward the west, much like *Pterostichus vulgaris*. The markedly mixed stock of south Scandinavia has evidently advanced to Vbt; the comparatively narrow gap between Vbt Vindeln and Nbt Ålvsbyn may therefore be a real one. No corresponding gap has been demonstrated in Finland.

What is the explanation for this northeastern, almost purely brachypterous stock? We might be able to assume that north Sweden was colonized earlier from the east than from the south. But the tip of this eastern advancing stock

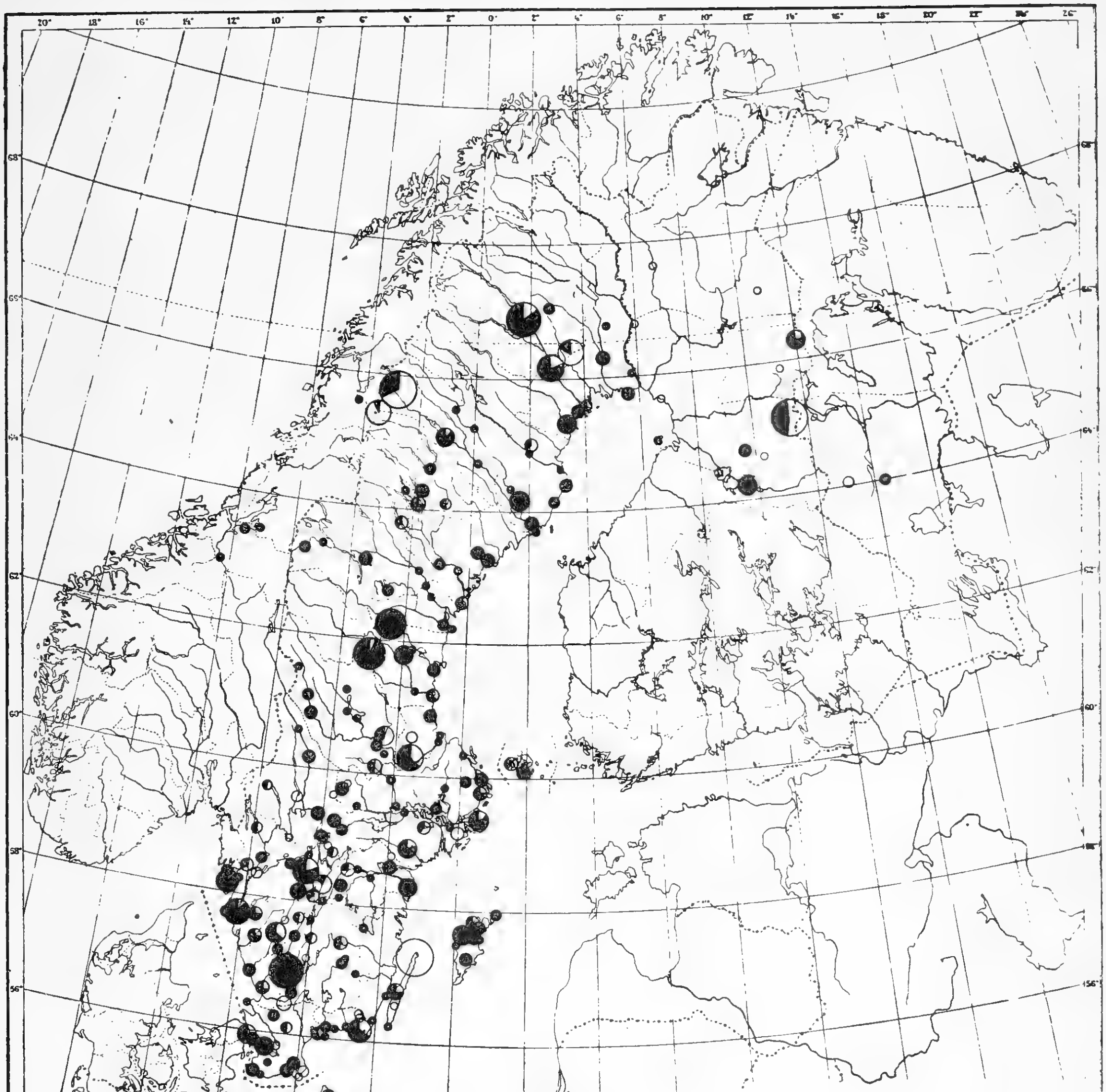
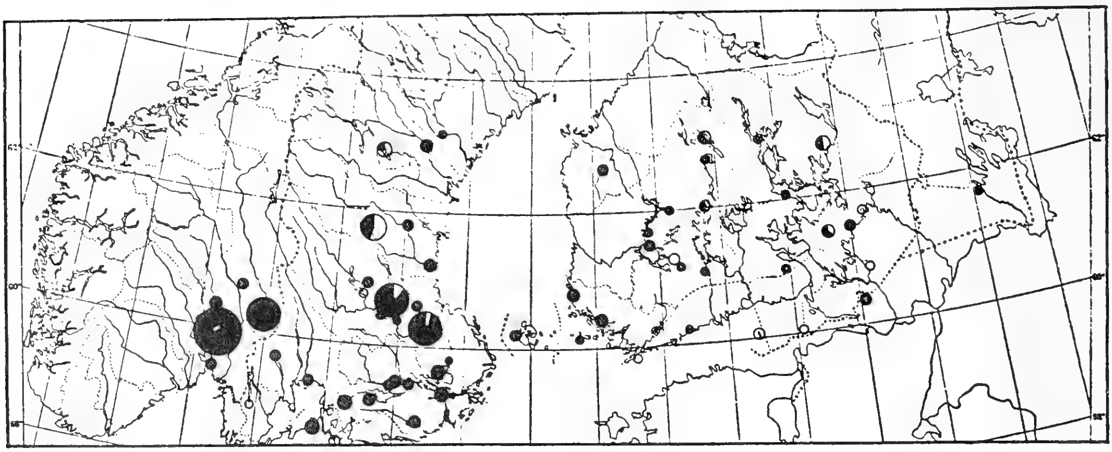


Fig. 40. *Bembidion lampros.*

Distribution map of wing-dimorphic forms in Sweden, in Norway north of latitude 63° N, and in Finland north of 64° N. For explanation see p. 367 and Fig. 28 (p. 368). The numerous macropterous specimens from north Öland originate from drift material.

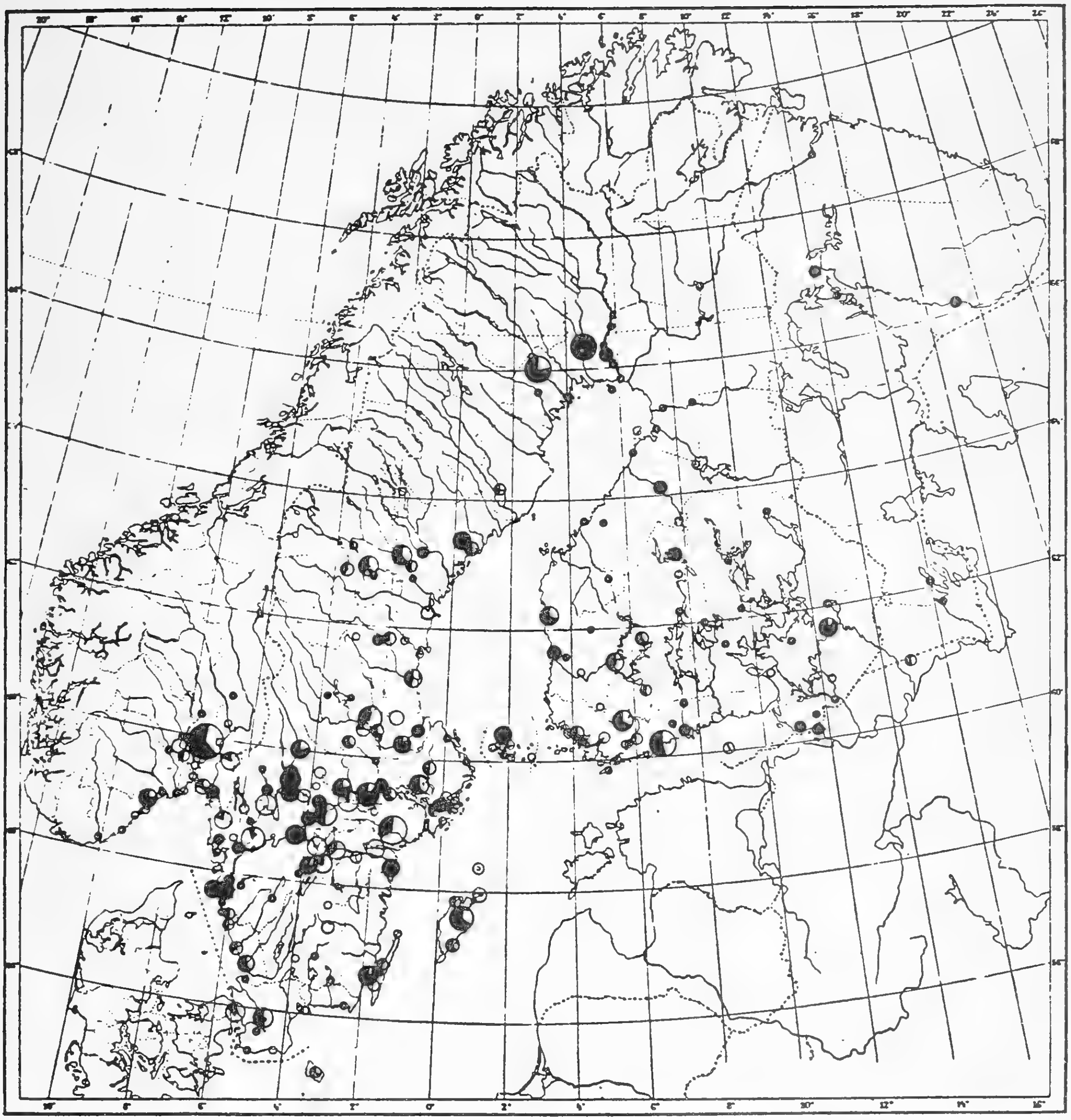
in Nbt, indicated by the occurrence of macropterous specimens cannot of course be blocked from advancing to the south by existence limits. It must be assumed that this stock has already advanced farther in its development toward brachypterism. It thus does not represent the northernmost outpost of the stock native to south Finland, which, especially in the southwest, reveals a strong macropterous component. But for this species it cannot be decided where in Finland the boundary between these two eastern stocks is to be drawn.

Pterostichus minor (Fig. 43) corresponds in important features. Only the presence of an actual gap in the distribution in north Sweden is doubtful (the Province of Ång has not been sufficiently explored). Instead this map
389 shows in a highly instructive way the difference between a group consisting predominantly of macropterous specimens immigrating late into central Norway (Trondheim region), and the north Finnish stock, which reveals its latent macropterism for the first time on the Swedish side. That this immigration was not very late is indicated by a fossil record of the species (probably from the early Littorina period) near Nbt Ålvsbyn (p. 671). The two arrows show the possible migration routes. Here too the insects immigrated to Finland by two separate routes, but once again it is difficult to draw the boundary between them in central Finland. This is easier for *Bembidion transparens* and *Pterostichus strenuus*, which are considered below in detail.



385 Fig. 41. *Bembidion gilvipes.*

Distribution map of wing-dimorphic forms (excluding south Sweden). For explanation see p. 367 and Fig. 28 (p. 368).



386 Fig. 42. *Bembidion guttula.*

Distribution map of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368).

In the case of *Bembidion nigricorne* (Fig. 44), which has very limited distribution, the conditions correspond in principle to the extent that in the northern subarea, which forms a peculiar belt across central Finland around latitude 65° N, only brachypterous individuals were found, but in south Finland and east Karelia, the macropterous form was also found. Both specimens found far from each other in central Sweden were brachypterous as well, but the only two localities on the west coast are represented by 3 macropterous individuals. In the north we apparently have the remains of a once continuous area which in the case of this stenotopic species of the open sandy *Calluna* heaths suffered greatly from the changes in the landscape and least of all secondarily in the climate.

Bembidion transparens (Fig. 45) shows total separation between a northern and southern stock in eastern Fennoscandia with a broad intervening gap. The latter has spread to central Sweden, where the Mälar lake region represents a secondary center. From here the species has dispersed in all directions, with a continuous decline of the brachypterous form; at the outer periphery (in the province of Gst, Vrm, Vgl, Hll, Ögl) the species is purely macropterous. Solitary records on Skå, Bornholm and Gotland are undoubtedly due to chance migration from the east. —The total area reveals still more clearly the eastern origin of the species. In central Europe the species has been found only along the German Baltic Sea coast, westward to Rügen*.

Especially interesting is the highly broken up area in north Fennoscandia.
392 Here the brachypterous form predominates to such an extent that macropterous specimens were found only at the periphery, partly in the west near Tromsdal (2 macropterous and 14 brachypterous specimens), and partly in the south at the northern end of the Gulf of Bothnia (2 macropterous and 7 brachypterous specimens). In the northeast, however, all 62 specimens studied were found to be brachypterous. That the north Fennoscandian stock as a whole does not represent an offshoot of the more southern stock is evident already from the usual distribution map (in Part II); but the dimorphic map also shows that the northern range must be considered the older of the two.

There is also an ecological difference between the two stocks. In the south it is a stenotopic lakeside species and occurs elsewhere, for example, along the seashore, only accidentally and solely in the macropterous form. On account of the instability of lakeside biotopes, selection there in general does not favor brachypterism. It is significant that in the Fennoscandian southern area of *Bembidion transparens* a marked preponderance of brachypterous species is found only around the large central Swedish lakes Mälaren and Hjälmaren,

*I was able to examine the wings of only a few specimens from the localities outside Fennoscandia: Pomerania, Köslin, 1 macropterous specimen, Wollin, 2 macropterous, 1 brachypterous specimen; eastern Prussia, Rauschen near Königsberg, 1 macropterous specimen; Poland, Pinsk, 1 brachypterous specimen; Siberia, Tobol, 3 macropterous specimens.

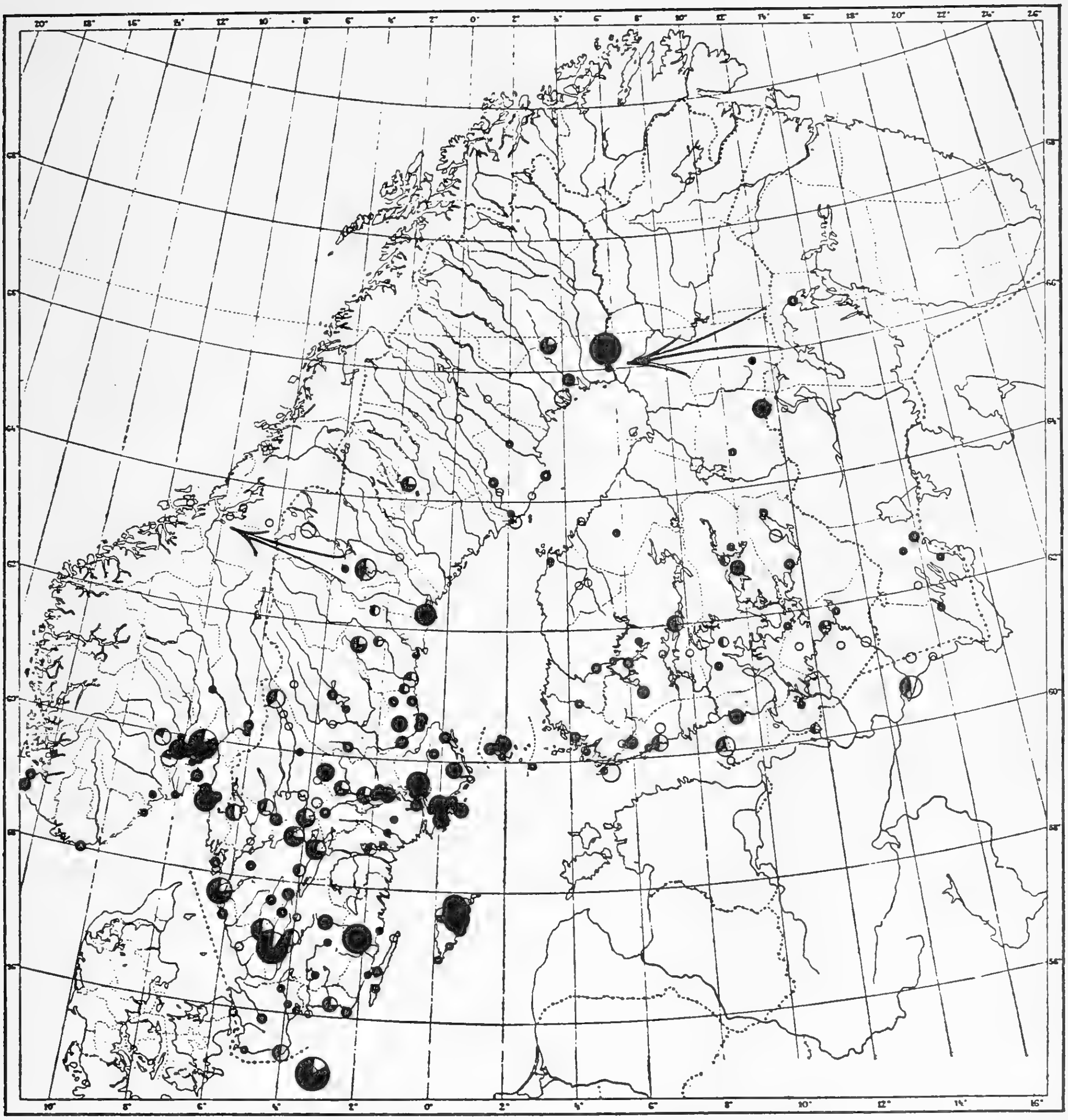
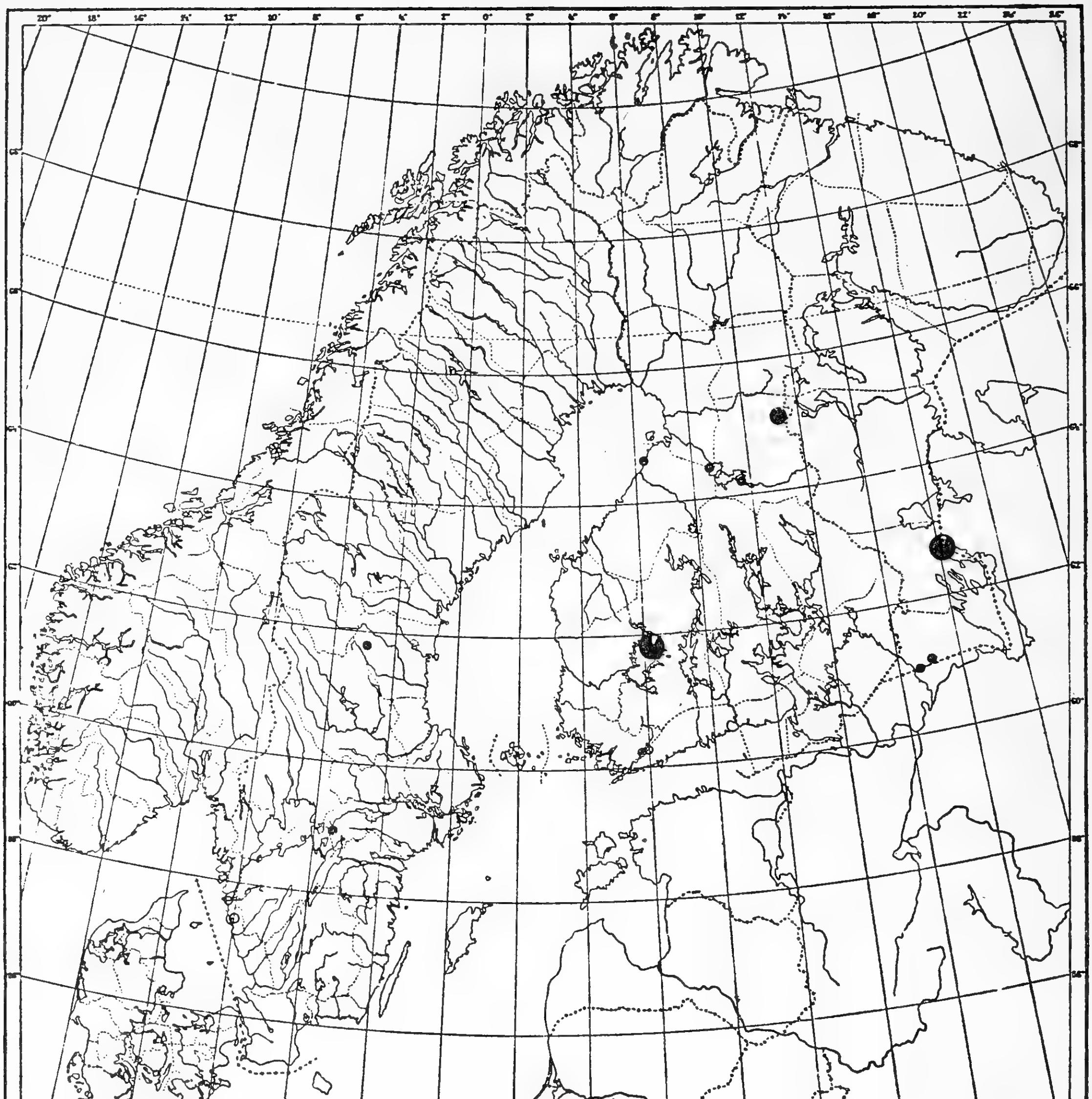


Fig. 43. *Pterostichus minor.*

Distribution map of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Arrows indicate presumed postglacial immigration routes.



390 Fig. 44. *Bembidion nigricorne.*

Distribution map of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368).

where the water level hardly varies (in part thanks to man-made regulation devices).

In the north the species is partly and apparently primarily an *inhabitant of the seashore*, which in any case was established in Lp Petsamo (Håk, Lindberg, 1933, p. 118) and in the southern part of the Kola Peninsula (Poppius, 1905, p. 91). With this mode of life, selection favors brachypterism (see p. 361), which has resulted in almost complete elimination of the macropterous form. In the inland of the north, dispersal of the species has thereby been greatly impeded. Especially watersheds have provided hurdles which to cross "is almost as difficult for a flightless riparian animal as it is for a fish"† (Lindroth, 1939, p. 262). The watersheds are thereby marked on the map. —In the cited work, where I briefly dealt with the species and supplied a map, I was very uncertain about the connection between the small subareas of the north. Later on, the species was found in considerable numbers near Ks Salla, close to the watershed between the Gulf of Bothnia and the White Sea. It seems thus very probable that the species reached the northern end of the Gulf of Bothnia from this region (and not from Norway) all the more as among the species considered above (and below) we repeatedly find examples of immigration by the same route, which was not clear to me at that time.

393 The Norwegian subarea, where the brachypterous form is still more prominent despite the most difficult possibilities for immigration, may actually be as isolated as the map suggests, and must be very old. It would be especially interesting if the somewhat doubtful record from 34 Lofoten (see Part I) could be confirmed.

The most important question is whether selection *during the postglacial period* can explain the preponderance of the brachypterous form in the north. Unfortunately we cannot attach too much importance to the fact that the northern Fennoscandian area appears completely isolated on the map even toward the east, offering no clue to the postglacial origin of the northern stock as a whole, —because northern Russia has been very poorly explored. On the other hand we can establish, that selection cannot operate more in favor of brachypterism in the north than in the south, as soon as the animal lives on the shores of *fresh-water*. But, if it is assumed that the northern stock originates entirely from seashore populations the situation is understandable. We must then go far back into the period when the species was pushed to the seashore—to the "Ice Age." The problem is summed up below (p. 412).

The central Swedish stock of *B. transparens* poses another problem of general relevance. The species is missing in all the older collections from this region. The earliest record dates to 1910 (Upl Uppsala), and presently this species is a characteristic animal of the eutropic *Phragmites* shores of the region! But if it actually immigrated so late, how has selection operated

†(Original German quotation translated into English; suppl. scient. edit.).

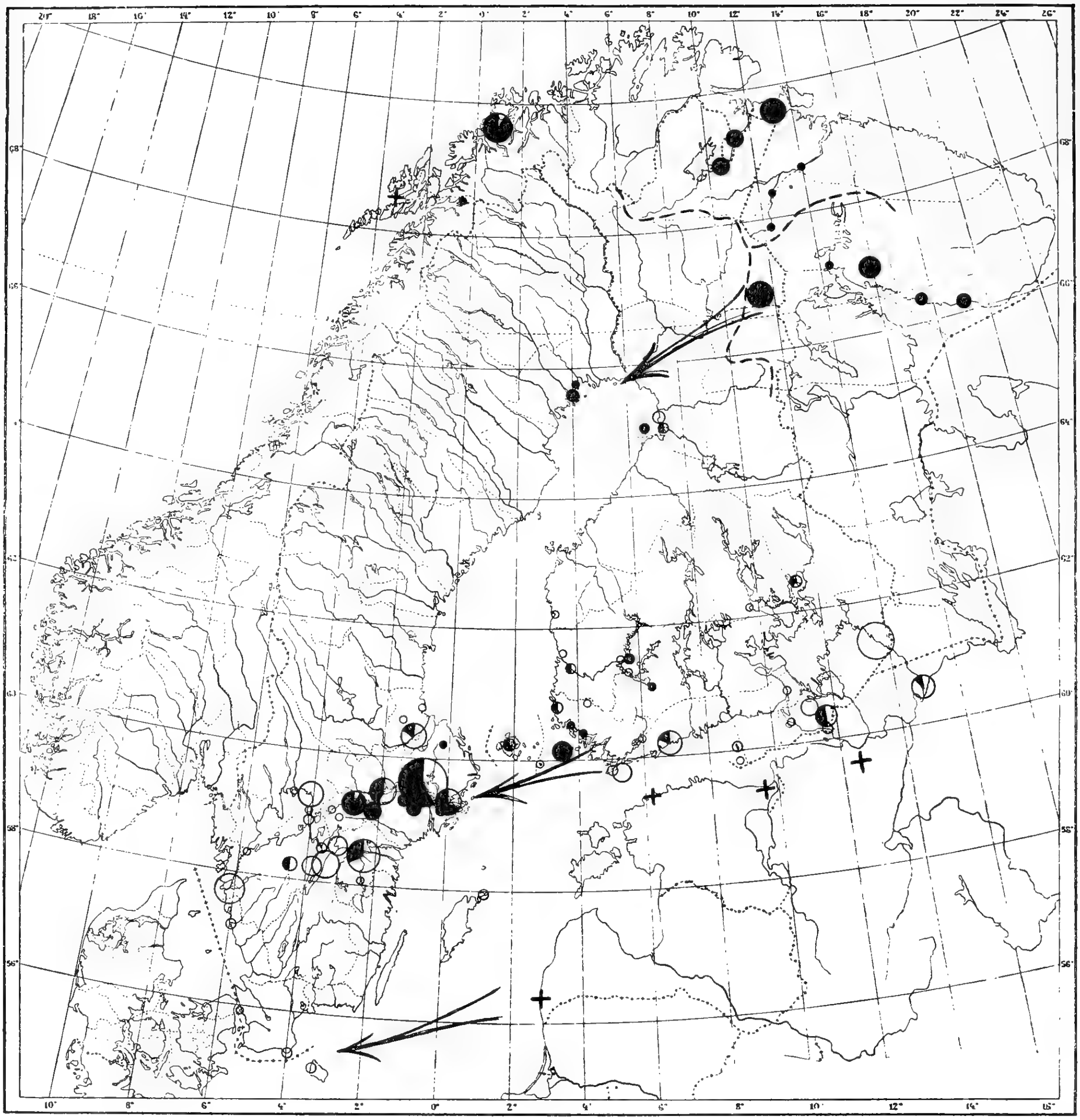


Fig. 45. *Bembidion transparens.*

Distribution map of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Crosses: No material available. Arrows indicate presumed postglacial immigration routes. In north Finland main watersheds are shown.

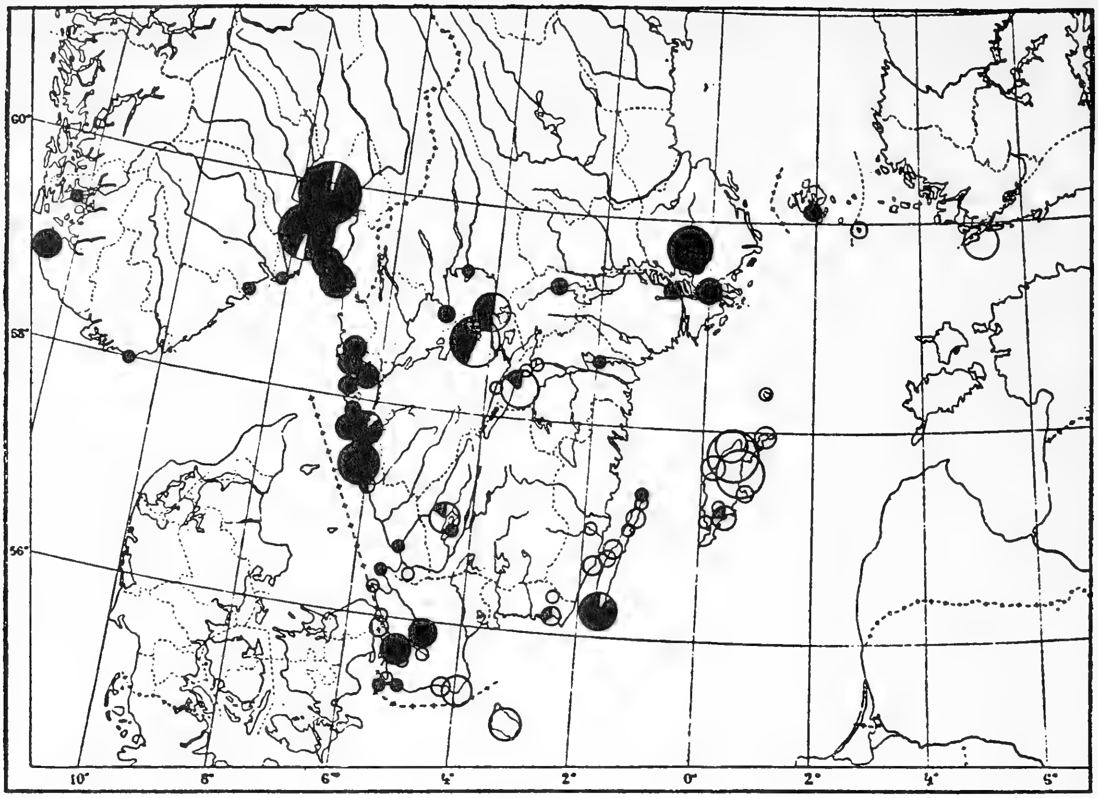
so rapidly in favor of brachypterism and how did the species arrive at all in its brachypterous form from the east, where no postglacial land connection spanned the Baltic Sea? Is it not more probable that Sweden was originally colonized by a pure (homozygous) macropterous stock, so that we have here a case of recurrent mutation, which originated on Swedish soil? Is this not supported by the isolated occurrence of 2 brachypterous specimens (among 2 macropterous ones) on Lake Hornborgasjön (Vgl)?

The problem cannot be solved without extensive experiments over many years. However, as a further example which indicates the same possibility, reference may be made to *Bembidion assimile* (Fig. 46). This species, primarily a seashore inhabitant which occurs in the west and on the large central Swedish lakes (excluding Vättern) predominantly in the brachypterous form, is mostly
394 macropterous in the southeast. This is particularly the case on Gotland, where among 63 specimens only one brachypterous specimen was found. Perhaps here, too, a recurrent mutation is in hand? For it seems improbable that selection along the seashores of Gotland would have operated differently from that along the west Scandinavian shores, on condition that the species arrived on Gotland right from the start in *both* forms.

Hypothetically one might be inclined to examine these difficulties in the case of *Bembidion transparens* and *B. assimile* (i.e. the isolated and rare occurrence of brachypterous specimens) on the assumption that brachypterism here is due to *a recessive* mutant. But the distribution in central Sweden of the two wing-dimorphic forms of *B. transparens* (and still more of *B. aeneum,* Fig. 49,
395 in which the rudimentariness of wings is similar) can be explained only under the presupposition that the macropterous forms are homozygotes.

However, there is a *third* possible explanation for the isolated and almost sporadic occurrence of brachypterous individuals in an otherwise purely macropterous population: that the brachypterous specimens are the *progeny of an immigrant macropterous female that had previously paired with a brachypterous male.* The question as to the extent to which fertilized females of carabids can actually fly is specially dealt with below (p. 595). Here it may be pointed out that the apparently purely macropterous populations at the periphery of the area of *Calathus mollis* or *C. erratus* clearly prove that such an event at least is not *common.* These species are pronouncedly xerophilous. —On the other hand it is perhaps no chance that the two species involved (*Bembidion transparens*, *B. assimile*), which might support the above assumption, are both *ripicolous.* Although flight after pairing is certainly unusual, one might imagine that species with this mode of life might be compelled to undertake an abnormal late flight (*after* pairing) if a small body of water at which edge they were living dried up (cf. *Bembidion doris*, p. 582).

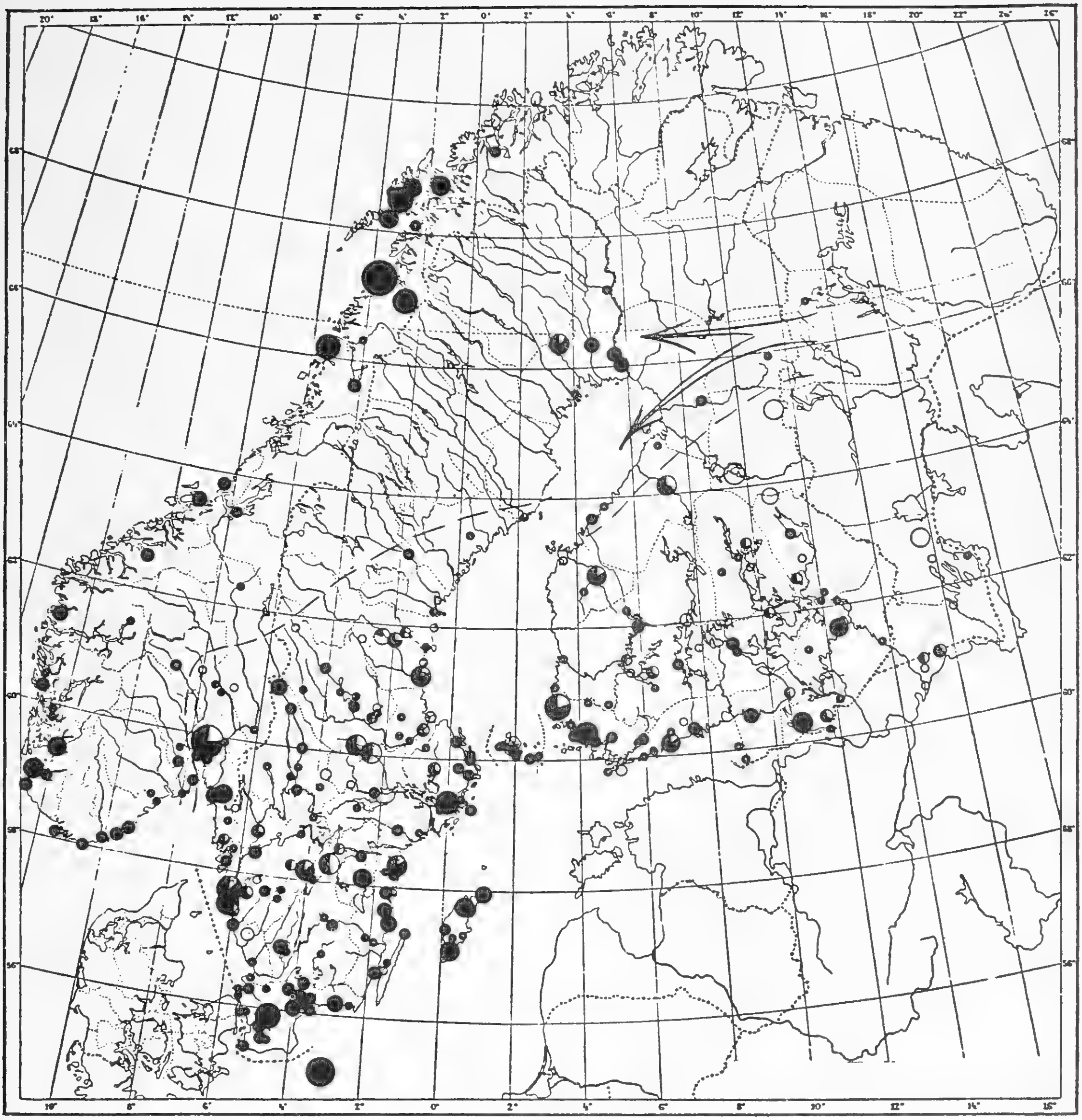
In the case of *Pterostichus strenuus* (Fig. 47) three immigration groups are evident. In south Sweden there is a large preponderance of the brachypterous form, but farther north as well as in Finland the macropterous form gradually



394 Fig. 46. *Bembidion assimile.*

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368).

increases in number. We have here two stocks which have immigrated during the postglacial period from the south. Their northern limit in Scandinavia is marked on the map by a broken line. It is not so clear in Finland, because here we have the same remarkable phenomenon as in the case of *P. minor* and *Bembidion guttula* (cf. also *Bembidion transparens* and *B. nigricorne*, as well as *Pterostichus lepidus* and *Carabus clathratus*): a marked, so to speak sudden increase in the number of brachypterous specimens at the northern end of the Gulf of Bothnia. The "brachypterous zone" in the case of *P. strenuus* is all the more evident because immediately to the south, in the inland regions of central Finland and east Karelia, there is marked preponderance of the macropterous form (between latitudes 62° and 65° N, 42 macropterous as
397 against 31 brachypterous specimens), found nowhere else in Fennoscandia.



396 Fig. 47. *Pterostichus strenuus.*

Distribution of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Presumed limits between three different stocks are shown with broken line.

This is another example of a separate stock that immigrated early from areas of the White Sea, which has also reached the Swedish province of Nbt. Characteristically, much as in the case of *Bembidion guttula* and *B. transparens*, only in this last area colonized the recessive macropterous gene manifests. *The postglacial immigration route from the east across Kuusamo and Salla has been of great importance.*

Still clearer are the conditions in Norway where, with the exception of a small region in the southeast, *only the brachypterous form has been found* (altogether 159 specimens examined). It is certainly impossible to claim that the macropterous gene has been completely eliminated here. But since it cannot be presumed that selection at least in the inland Norway is presently operating in a different way than in the corresponding parts of Sweden or Finland, it must be concluded that the Norwegian stock of *P. strenuus*, at least in the west and north, *did not immigrate postglacially from Sweden and that it, on the other hand, is very old* in order that the elimination of the macropterous form has progressed to such a degree, whereby the dispersal capacity of the animal was greatly reduced as well.

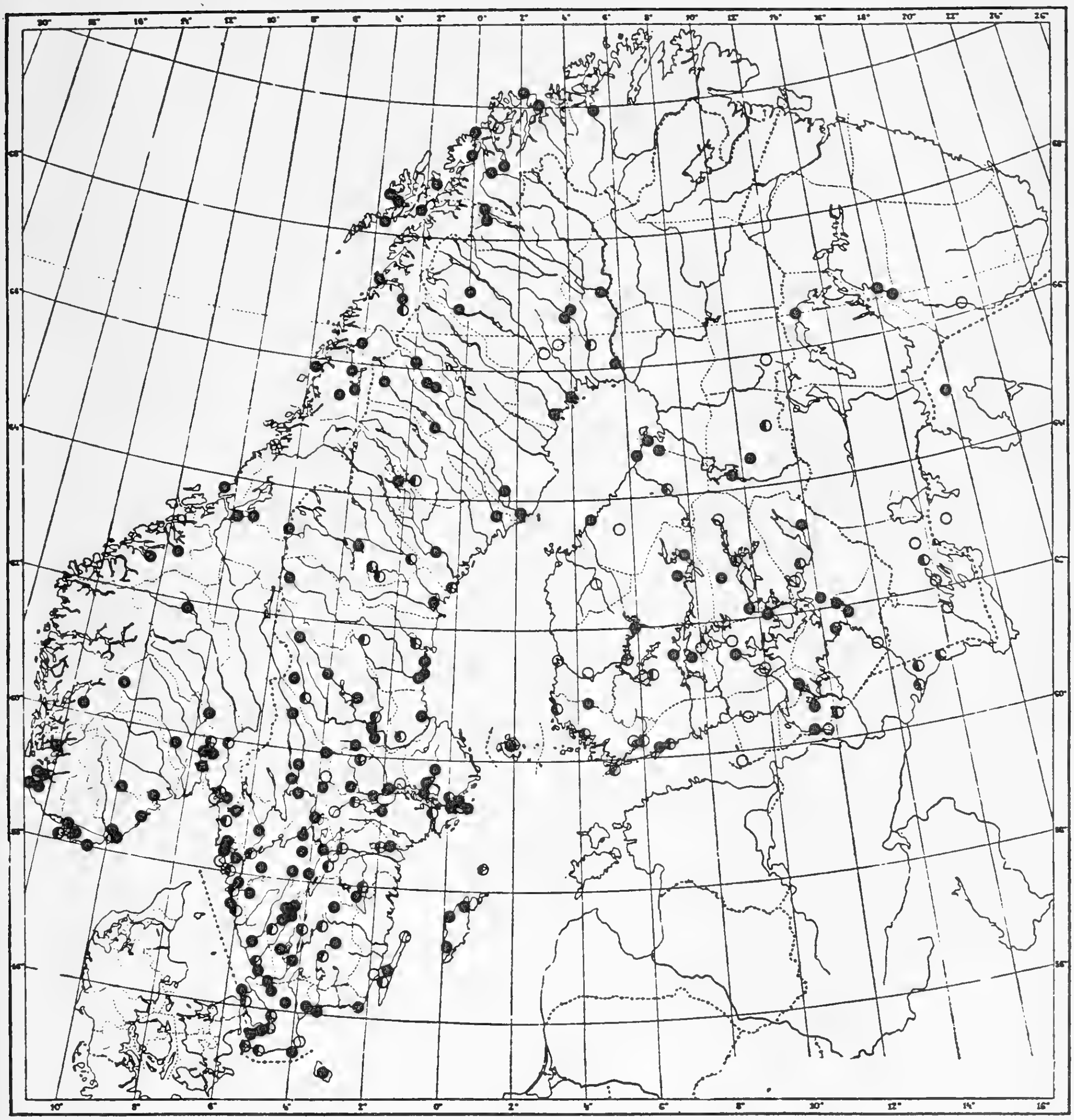
This brings us to the most important result of the present study of dimorphism, the history of the west Scandinavian faunal element. This problem will now be taken up with the help of further examples.

The map of *Bradycellus collaris* (Fig. 48) is not quantitative. Each locality is marked only to indicate whether brachypterous (black), macropterous (blank), or both forms were found. The reason is partly that from certain localities (in connection with crossing experiments) so much material was available to me (for example, 268 specimens from Upl Djursholm) that the usual depiction by circles was not practicable and partly that the macropterous specimens are mostly so rare that their distribution can be expressed clearly only by the method used here.

In eastern Fennoscandia both forms occur side-by-side almost everywhere. The macropterous form was found even on the southern side of the Kola Peninsula. Hence nothing contradicts a uniform postglacial immigration to this part of the region.

In Scandinavia the macropterous specimens decrease in number toward the north and markedly toward the west. In Norway the conditions remind very much those of *Pterostichus strenuus*, with the important restriction that the
399 macropterous form was not so thoroughly eliminated by selection. Still, only 4 macropterous specimens among 114 brachypterous specimens were found there, excluding the southeast (as in the case of *Pterostichus strenuus*). It is moreover interesting that this predominantly brachypterous western stock has also spread to the Swedish fjeld regions, where so far only brachypterous specimens have been found from northern Dlr to Tol.

The map of *Bembidion aeneum* (Fig. 49) is schematically fairly clear. The usual distribution map (in Part II) already shows the strong geographical iso-



398 Fig. 48. *Bradycellus collaris.*

Distribution map (non-quantitative) of wing-dimorphic forms. Blank circles—Only macropterous specimens; Black circles—Only brachypterous specimens; Divided circles—Both forms.

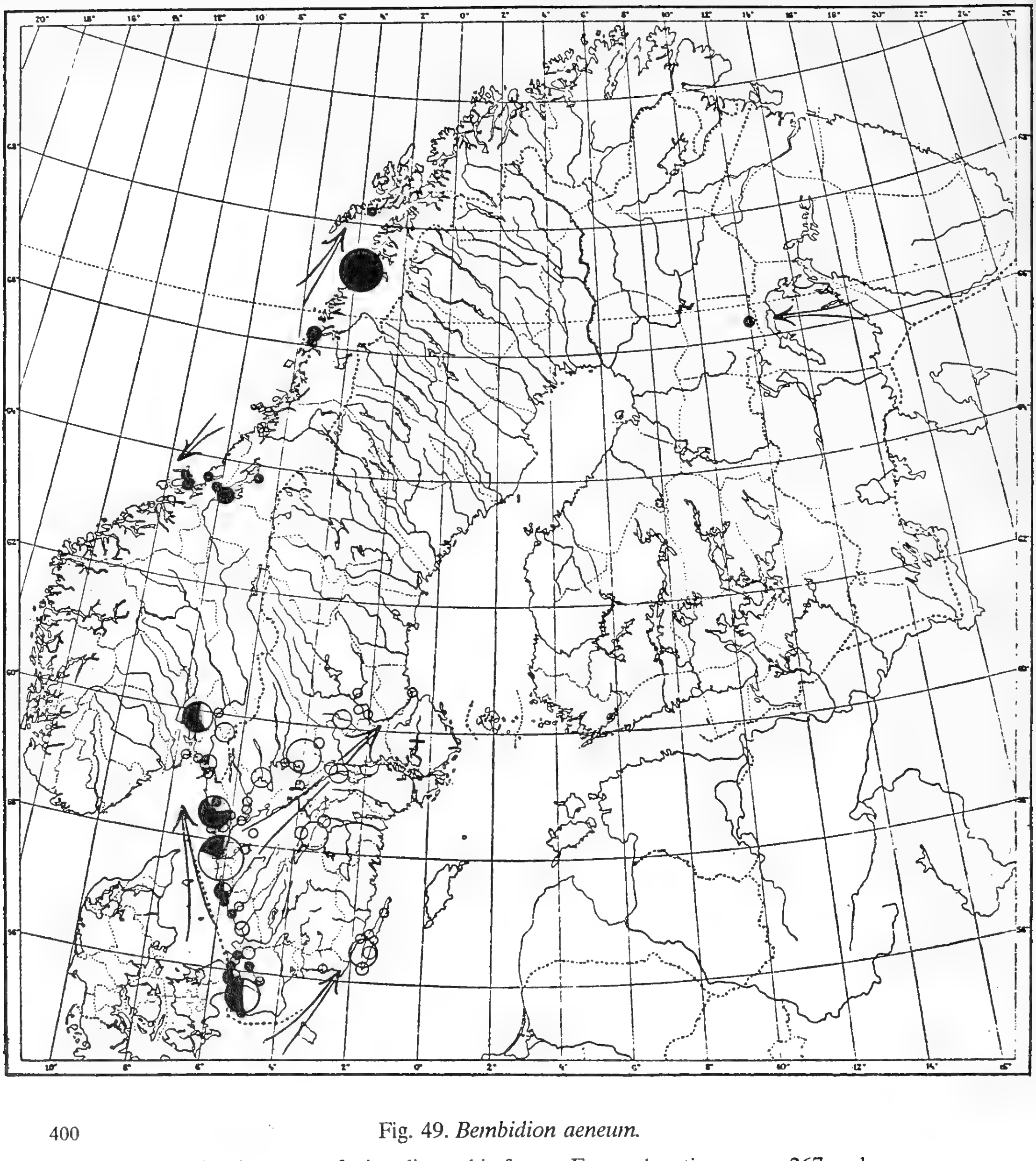


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Fig. 49. *Bembidion aeneum.*

Distribution map of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Cross indicates Upl Uppsala, from which no material was available. Arrows indicate presumed postglacial migration routes.

lation of the western Norwegian subarea, which must have its own history. The dimorphic map clarifies the recent postglacial history throughout the region.

In the south, in spite of its wide distribution, the species occurs as an original inhabitant of the seashore. Here, from southwestern Skå to the Oslo region, both forms live side-by-side in nearly equal numbers (specimens studied: 78 macropterous, 70 brachypterous). Only in Skåne, near Lund on the bank of the River Höje-å and near Klippan on the Rönne-å, were brachypterous specimens found at some distance (respectively 8 and 24 km) from the sea, in addition to one intermediate (flightless) specimen on the south shore of Lake Bullaren in Boh (15 km from the sea). All other Scandinavian inland records, as well as those along the coast in the southeast (Ble, Små, Öld), represent macropterous specimens. They are the result of a late immigration from the southwest and the sifting out of flying animals from the mixed populations of the seashores. This route, obliquely across central Sweden through Vgl to the Mälar region, has been used by many other southern immigrants with flight capacity, especially the species associated with loam (p. 717). It may appear strange, that unlike *B. assimile*—the dimorphic map (Fig. 46) is otherwise similar—*B. aeneum* strangely failed to establish "relict stocks" of the brachypterous form on the shores of the large central Swedish lakes. A possible explanation is that during the Yoldia period the southern *aeneum* stock had not yet extended so far north.

In the strangely isolated area of western Norway only brachypterous specimens (61 of them were examined) were found. Naturally we cannot decide whether the macropterous gene has completely disappeared there, but in the context of dispersal biology the species is evidently to be considered brachypterous here. Since it is moreover a stenotopic seashore inhabitant it is not surprising that it has remained static. We have here the oldest Scandi-
401 navian stock of *Bembidion aeneum*, *which cannot have immigrated during the postglacial period.*

However, the strangest record of *Bembidion aeneum* is from Ks Paanajärvi lake, where 2 specimens were discovered in different years. Both are brachypterous; there is no question of accidental occurrence. In the preliminary treatment of this species (Lindroth, 1939, pp. 262–263), I assumed immigration from the east. When later on the great importance of this immigration route via Salla and Kuusamo for a whole series of species became clear (see *Pterostichus strenuus*, and summarizing discussion on p. 724), this assumption was greatly strengthened. Probably the species still lives on the shores of the White sea, which have unfortunately been very inadequately explored, especially in the south.

Before looking at the dimorphic map of *Bembidion grapei* (Fig. 50) it is advisable to study the usual distribution map (in Part II) more closely. What conclusions could have been drawn concerning the immigration of this species on the basis of this map alone? It is a picture of a widely distributed species

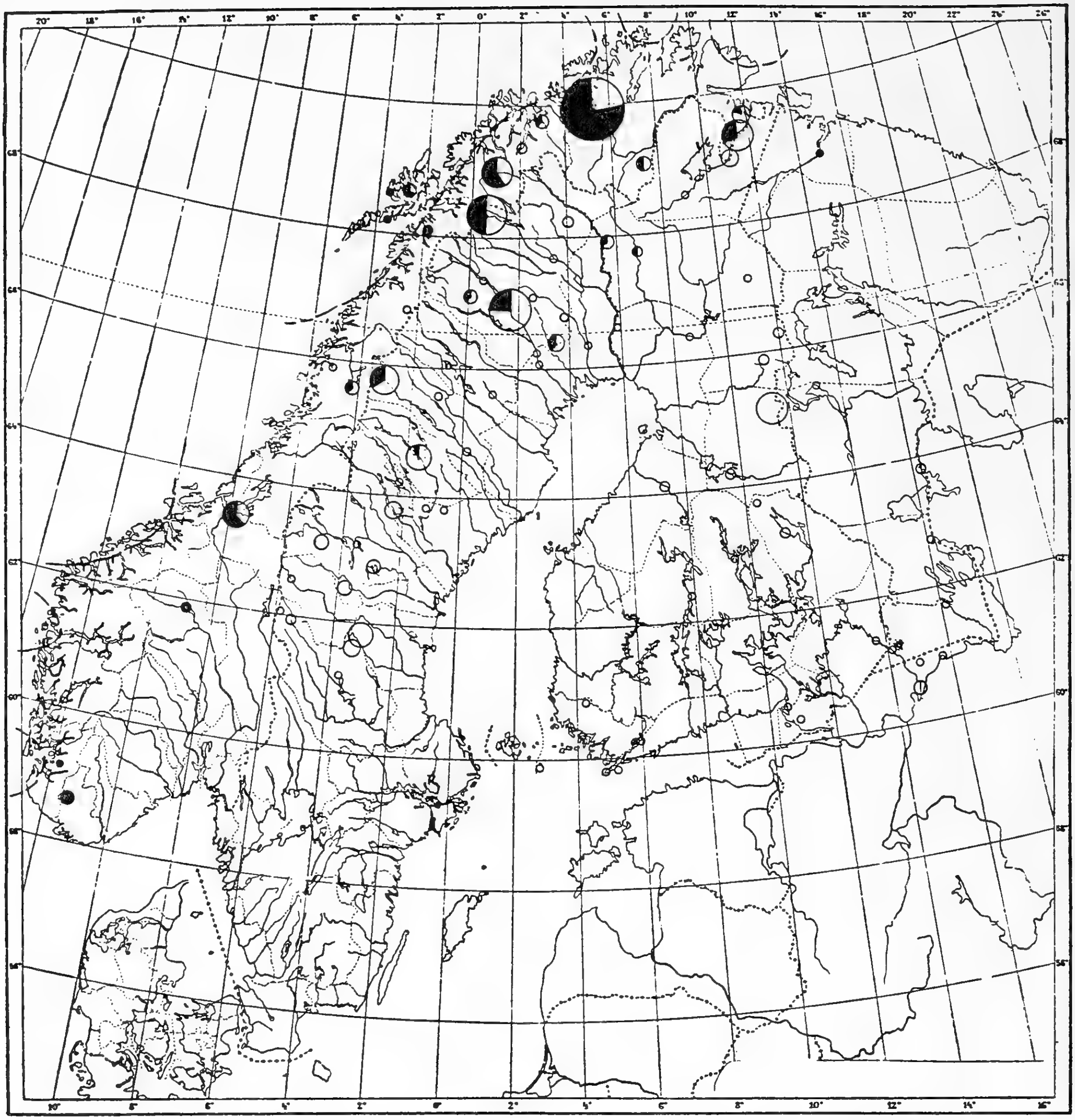

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Fig. 50. *Bembidion grapei.*

Distribution map of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Limits of presumed Würm refuges in Norway (after Nordhagen, 1933, 1935) are indicated.

of the high boreal coniferous forest area, somewhat of the type of *Pterostichus adstrictus* or of *Pelophila borealis*. The apparently continuous distribution over the whole of Finland until the southeast of Karelia suggests a firm connection eastward through Russia to Siberia, thus a component of the "Siberian woodland fauna" immigrated during the postglacial period. Only the more or less complete absence from the Kola Peninsula may appear strange, as also, particularly, the isolated localities of the south Norwegian records.

But the dimorphic map gives a completely different, so to speak reverse picture. In the whole of eastern Fennoscandia, with the exception of the far north (north of latitude 67° N) only the macropterous form (53 specimens) has been found, and the same in Sweden south of latitude 64° N (40 specimens). However, toward the north and especially the west, that is in Norway, the brachypterous form gradually increases in number. Symptomatic was extensive material (80 specimens) from 38 Alta, which comprised 62 brachypterous and 18 macropterous specimens.

Is it now possible, if only from a purely theoretical viewpoint, to regard *Bembidion grapei* as a postglacial immigrant of Fennoscandia, in view of this distribution of short-winged and long-winged individuals of the species? Like the cat around the stew pot, we have been going round this question so far. Now we must seriously take it in hand.

403 The concentration of the brachypterous form of *B. grapei* in north and west Fennoscandia could give rise to any of the following attempted explanations (cf. a similar formulation of the question for *Calathus mollis*, p. 370), provided that the character is genetically determined.

1. The species immigrated to Fennoscandia exclusively (or predominantly) in macropterous form during the postglacial period, and the brachypterous form in the west and north arose thereafter (or enriched):

   a. by recurrent mutations;

   b. by a particular influence of the selection; —or

   by a combination of both factors.

2. The regions with predominantly or exclusively brachypterous populations were colonized earliest. These are Ice Age refuges, from which a postglacial emigration took place into the regions once covered with ice (hence predominantly to the east).

1a. *Recurrent mutations* have been experimentally established, especially in *Drosophila*; of the known wing-reducing mutation "vestigial" at least 29 alleles are known (thus phenotypically not or hardly separable), almost all in the same locus (chromosome 2). Earlier (p. 393) we hypothetically set up the possibility of recurrent mutations in *Bembidion transparens* and *B. assimile*. However, who wishes to explain the occurrence of brachypterous *B. grapei* only in certain areas of Fennoscandia by mutations "in situ", must ascribe the definitive role to environmental factors in west Scandinavia, not only for the species in question but for all the other species here considered that attained

maximum brachypterism in these regions. One would have to maintain that the west Norwegian climate (since other environmental factors do not come into question) would have caused a similar (or corresponding) mutation in an entire series of species. But this totally contradicts our present experience, achieved experimentally and theoretically, on the nature of mutations. —More important is the finding that by mutation alone, however high its frequency owned is, suppression of the "normal type" cannot result. The more or less complete preponderance of the brachypterous form in a subarea of the species can be explained *only by selection* (whether this has taken place within the limits of the area or outside it before the immigration).

404 1b. *Some particular effect of selection* in west Scandinavia deserves serious consideration. One might thus surmise that *B. grapei* immigrated during the postglacial period (for instance, from the east along the northern margin of the shrinking ice, as soon as the coastal areas became ice-free) in macropterous form (possibly, but improbably, with a slight admixture of the brachypterous form). After the origin of the brachypterous gene by mutation, selection in the west should have operated strongly in favor of brachypterism. One might remember in this case the exposed location of the largely unforested coastal areas of Norway and the high frequency of atmospheric minima with the attendant, often strong winds.

In the case of *B. grapei* we have first of all to notice that the species was found within the region not above the timber line (see Part I) and does not live at all in very exposed places, but mostly in association with forest and undergrowth. And if we transfer this observation on species like *Bradycellus collaris* and particularly *Notiophilus aquaticus* (see below), we come across the unexplained phenomenon that the brachypterous form on the Swedish side as well in the fjelds as in the valleys, shows an equally strong preponderance. And the climatic conditions here are totally different. Large continuous subareas of a species, inhabited predominantly or (apparently) exclusively by the brachypterous form, *cannot have arisen solely by selection operating at present.* For none of the 3 species mentioned here (even the little *Pterostichus strenuus*), ecologically considered, has such a stenotopy that flight capacity could have dangerous consequences (for *Bembidion aeneum*, which is associated with the seashore in west Norway, it might). And a positive selection value must be ascribed to the brachypterous form (more correctly: denied to the macropterous form), if the short postglacial period has sufficed to allow the origin of a mutation (see calculations on p. 365) and an increase up to preponderance (in the case of *Pterostichus strenuus*, *Bembidion aeneum*, *Notiophilus aquaticus* apparently up to 100% strength).

We must also refer to *Calathus erratus* and *Pterostichus vernalis*, in which the *Macropterous* form is predominant in west Norway. Together they show that the climate in these parts does not favor "*a priori*" the brachypterous form of a dimorphic species.

2. The preceding account has probably shown that the geographical distri-
405 bution of the two wing-dimorphic forms of *Bembidion grapei* (besides various other species) cannot be explained by the currently prevailing conditions of climate, etc. We must go back to the last glaciation (Würm). Accordingly the map shows the Würm refuges presumed particularly by Nordhagen (1933, 1935) (but also cf. map in Fig. 111, p. 775). Supposing that *B. grapei* "wintered" in some (or all) of the ice-free coastal regions, the map is readily understandable without any hypothetical construction. The rule first formulated for *Calathus mollis* is applicable: At the periphery there are macropterous specimens and a preponderance of the brachypterous form is to be found in the regions colonized early.

Finally the question remains whether the entire Fennoscandian area of *B. grapei* has arisen by emigration from the Norwegian coastal refuges. Inasmuch as to the east, south of the White Sea, there is probably a continuous distribution across Russia (see Part I), the answer is not forthcoming. Now Poppius (1911, p. 36) published an early postglacial subfossil record ("Dryas zone") of this species from Finland Ik. Unfortunately it was not possible to examine the elytron that he studied (probably in MH), and the determination is certainly not definite. However, the find would not be surprising, since it appears most probable, that from the start south Finland received its *grapei* stock from the east or south during the postglacial period. Otherwise the dispersal of the glacial stock proceeding south would have been considerably more effective in Finland than in Scandinavia, where, especially in south Norway, the degree of colonization is perceptibly low. This last condition will be explained if future study of more numerous material from Norway south of latitude 62° N actually confirms the total absence of the macropterous form here.

The last two dimorphic maps show how even in the case of more or less universally distributed species, whose geographical distribution in itself provides no clues, the mapping of wing-dimorphic forms may be "revealing." The species in question both belong to the genus *Notiophilus*.

Since the publication of Part I many new records of *Notiophilus biguttatus* have come in, and a couple of records noted there have turned out to be uncertain (see Supplement to this part). It seemed best to give a revised "usual" distribution map (Fig. 51) to provide an instructive comparison with the dimorphic map (Fig. 52).

408 *Notiophilus biguttatus* is almost universally distributed in Fennoscandia. As a pronounced forest species, which occurs very sporadically and possibly accidentally in the *Regio alpina*, it is missing from the high mountains and the tundra. More noteworthy is the gap in north Finland, which also extends into the wooded regions of the Kola Peninsula.

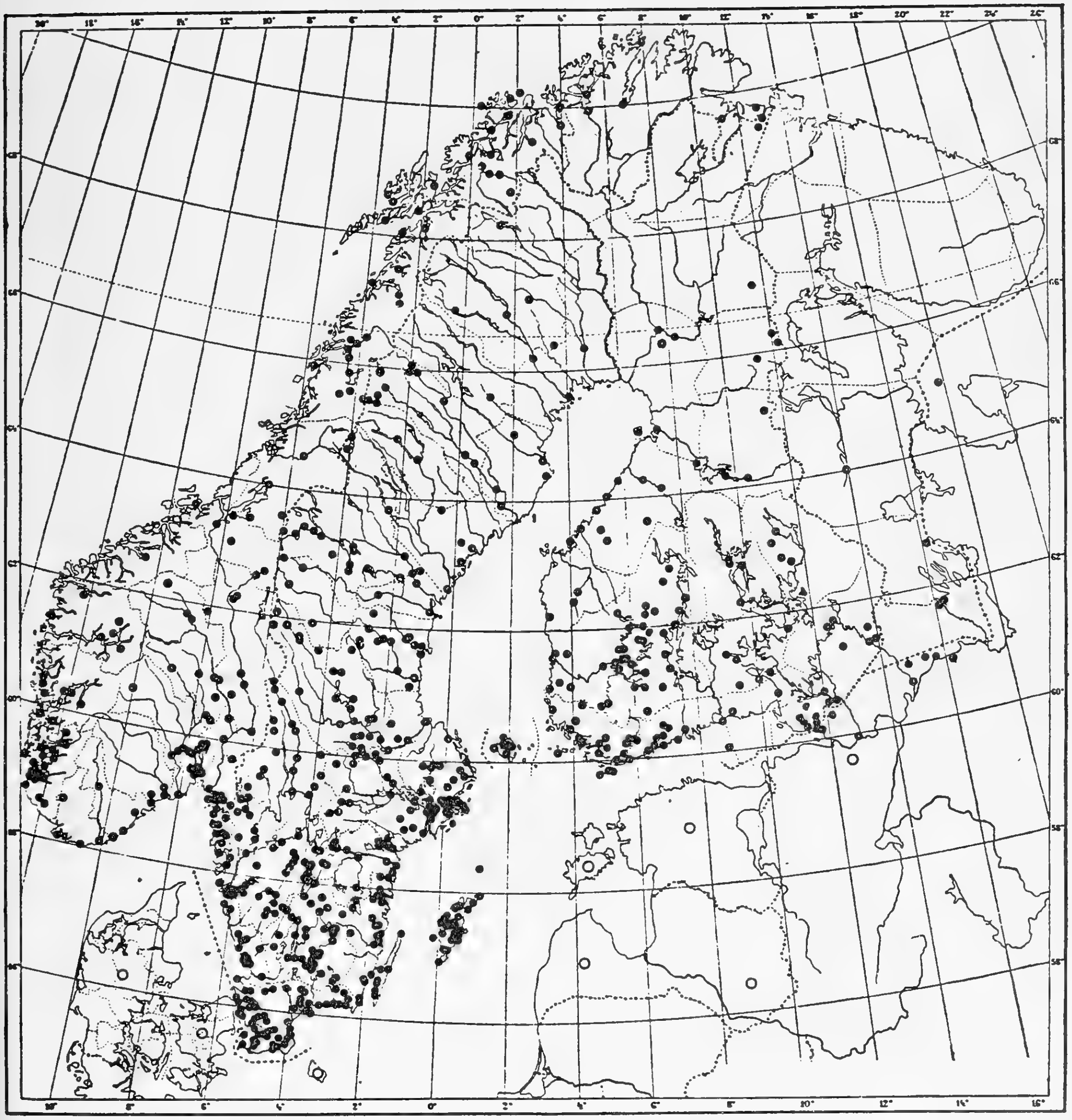
Such a map gives no idea of the immigration routes. The dimorphic map does. The distribution of the two forms becomes clear from a rough compari-

son between the latitudinal zones of the three countries (excluding the Baltic Sea islands):

	Macropterous specimens	Brachypterous specimens	Index = (macropterous/ brachypterous)
Finland			
South of latitude 62° N	69	27	2.55
Between latitude 62° N and 64° N	32	12	2.66
Between latitude 64° N and 66° N	12	4	3.0
Between latitude 66° N and 68° N	4	1	4.0
Sweden			
South of latitude 58° N	66	22	3.0
Between latitude 58° N and 60° N	52	26	2.0
Between latitude 60° N and 62° N	41	59	0.7
Between latitude 62° N and 64° N	14	32	0.44
Between latitude 64° N and 66° N	15	31	0.48
North of latitude 66° N	15	5	3.0
Norway			
South of latitude 60° N	26	46	0.57
Between latitude 60° N and 62° N	3	26	0.12
North of latitude 62°N	4	105	0.04

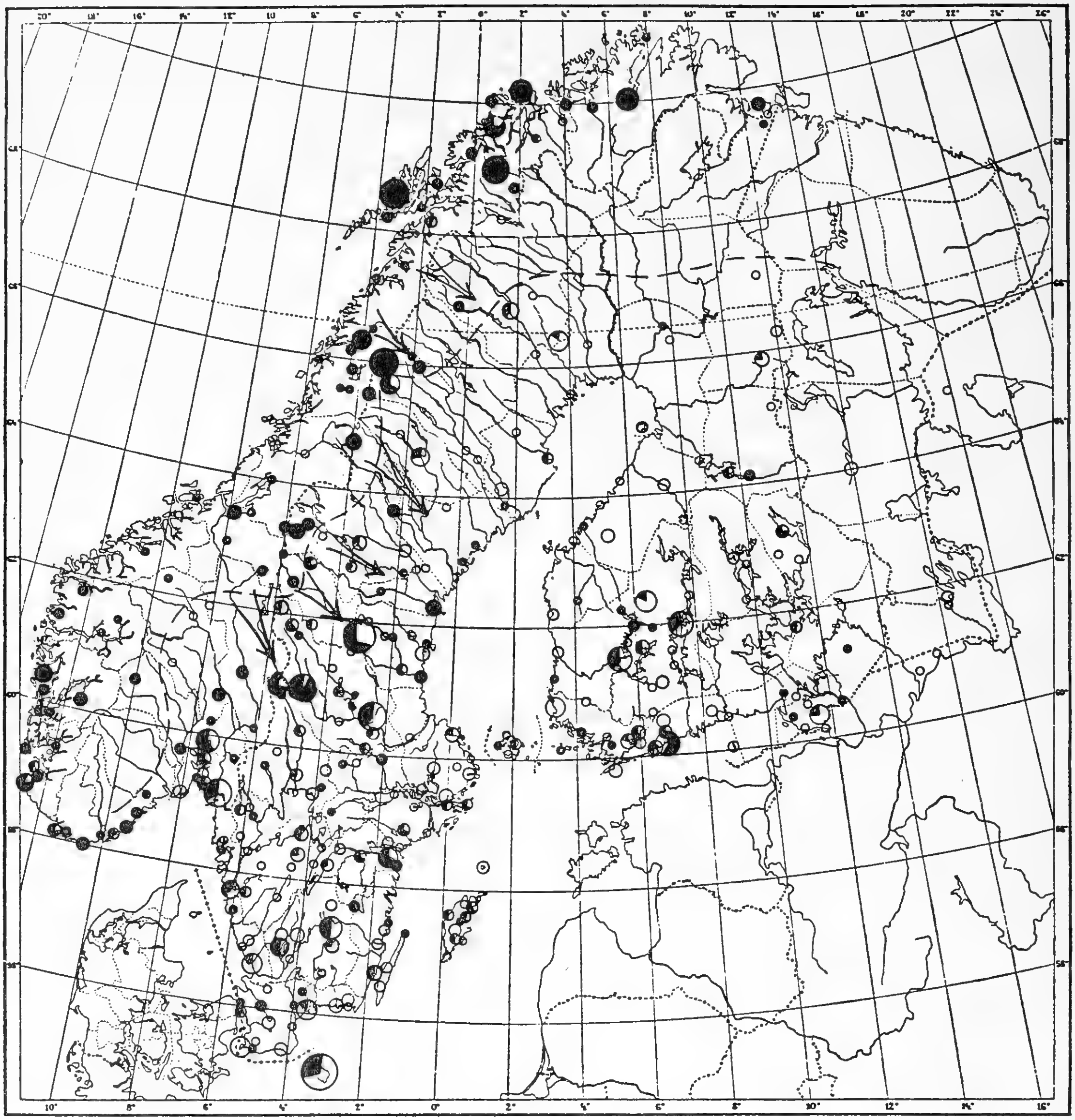
In Finland the distribution is easily understandable. To the north the brachypterous form gradually declines in number. The map very much gives the impression of a stock that immigrated during the postglacial period from the south. The only exceptions are the two localities in Petsamo, which have connection with the Norwegian area.

In Sweden the conditions south of latitude 60° N and in the far north (beginning from latitude 66° N) largely correspond with those in Finland. But in the rest of Sweden the brachypterous form preponderates, with increasing number to the west. These are the parts connected with Norway by wooded regions or, in the north, by numerous wooded passes.



406 Fig. 51. *Notiophilus biguttatus.*

Completed and corrected distribution map (cf. Part II of this book).



407 Fig. 52. *Notiophilus biguttatus.*

Distribution map of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). Minimum limit of postglacial stock westward and northward is indicated by a broken line. Arrows indicate migration routes of the Würm "overwintering" element.

Finally, in Norway the macropterous specimens play a significant role only in the extreme south, chiefly in the coastal regions. In all other parts they occur sporadically or are apparently totally missing in large regions.

409 This colossal west Scandinavian stock, in which the macropterous individuals have been nearly eliminated, has undoubtedly arisen through Würm hibernation. This species is especially interesting because the above-mentioned old stock has met with the postglacial immigrated stock on a broad front. Study of more material—more than was available to me—would certainly establish such origins of the individual populations in this mixed zone. —I had assumed that the macropterous specimens, wherever they were still found, must have had a southern, postglacial origin, in other words that the interglacial stock had become "purely" brachypterous by selection (and finally by accident; see p. 365). A later study of material of the same species from Iceland, where the species was certainly a Würm hibernator as well (Lindroth, 1931), showed, however, that there, too, the macropterous form had not been completely eliminated (four macropterous among 148 brachypterous specimens). So it is impossible to establish the outermost limits of the postglacial immigration in Scandinavia by means of the isolated, sporadically occurring macropterous specimens in Norway. Such a conclusion would be justified only if they occurred regularly. The broken line on the map thus is the presumed *minimum limit* of the postglacial stock to the west.

However, the regions of Scandinavia where the brachypterous form shows a distinct preponderance (established by a study of sufficient material!) must have been colonized to a greater or lesser extent starting from Ice Age refuges. The arrows on the map show such emigrations to the Swedish region.

Notiophilus aquaticus (Fig. 53) is the most widely distributed of all Fennoscandian carabids. It is the only species that lives uninterruptedly from southernmost Skane to the high alpine zone of the fjelds and the tundra of the Kola Peninsula. Ecologically too it is very eurytopic, but it cannot be considered ubiquitous because it avoids wet places and densely wooded regions.

Therefore one cannot imagine a distribution map that is *less* appropriate to speculation about immigration routes. The accumulation of points, especially in certain fjeld regions, is greatly explained by more thorough exploration and cannot be considered as centers."

Much more instructive is the dimorphic map, which largely corresponds with that of *N. biguttatus*. We find the macropterous form distributed fairly
411 uniformly over most of Finland, over Sweden (with the exception of the fjeld regions), and finally in southeastern Norway. In general, however, it occurs in a pronounced minority and is best represented in Swedish Norrland. The most important difference with *N. biguttatus* is that *only brachypterous specimens have been found* on the west coast between 6 Stavanger and 40 Varanger, as well as in a broad adjoining region which also touches Sweden from Hjd

onward, and in the Kola Peninsula (with the exception of the southwest). This is the "interglacial stock," from which the macropterous form seems to have been completely eliminated. In *N. biguttatus* we found that the interglacial stock had not completely lost the macropterous gene, that this even manifested itself phenotypically in 4–5% of the individuals as a result of crossing between heterozygotes. In *N. aquaticus* the selection has proceeded farther, so that among 400 specimens from the "purely" brachypterous region in west and north Fennoscandia, no macropterous specimen was found. The reason may be *on the one hand*, that the "initial stock" of *N. aquaticus* was brachypterous to a greater extent than in *N. biguttatus*, which is indicated by the condition of the postglacial stocks of the two species (perhaps by the higher probability of emigration of the brachypterous form of *N. aquaticus* to the refuges at the beginning of the Würm period, given the pronounced resistance of this species to adverse climate). *On the other hand* it may be, that selection in the case of *N. aquaticus* favored the elimination of macropterous specimens, since this species lives in rather exposed places, whereas *N. biguttatus* lives mainly in localities protected by woodland or bushes.

Evidently we can never *prove* that the brachypterous interglacial stock of *N. aquaticus* is completely homozygously brachypterous. But since macropterous specimens in this region occur at most completely isolated, it is at any rate justified in taking the broken line on the map (Fig. 53) as the *maximum limit* attained by the stock that immigrated in the postglacial period. This can be fixed with greater certainty than the corresponding minimum limit of *N. biguttatus* (Fig. 52). But it is not possible to follow the sporadic advances of the interglacial stock to the east as in the case of *N. biguttatus*, on account of the preponderance of brachypterous specimens even in the postglacial stock of *N. aquaticus*.

412 What remains to be done is to examine more closely the Ice Age conditions, which for many species caused selection in favor of brachypterism, and furthermore to answer the question why dimorphic species generally seem to be favored in an area glaciated during the Quaternary period (cf. p. 364).

The Fennoscandian Würm refuges, which are treated in greater detail elsewhere (pp. 752 ff.), are now generally believed to have been ice-free coastal regions, situated—in any case predominantly—in western and northern Norway. The peaks in the mountains ("nunataks"), completely surrounded by ice, biologically had at the most a very subordinate role. The coastal refuges were comparatively small, surrounded on all sides by obstacles (from the viewpoint of terrestrial biology), namely ice and sea. They were like isolated islands or mountain peaks, encircled by uninhabitable areas, and the fauna, like that of the above-mentioned areas, was subject to a selection that favored flightless individuals, forms and species. As soon as an insect in these places took off into the air there was the danger of its arriving, actively or passively, on the ice or in the sea, resulting in death by freezing or drowning. The latter eventuality

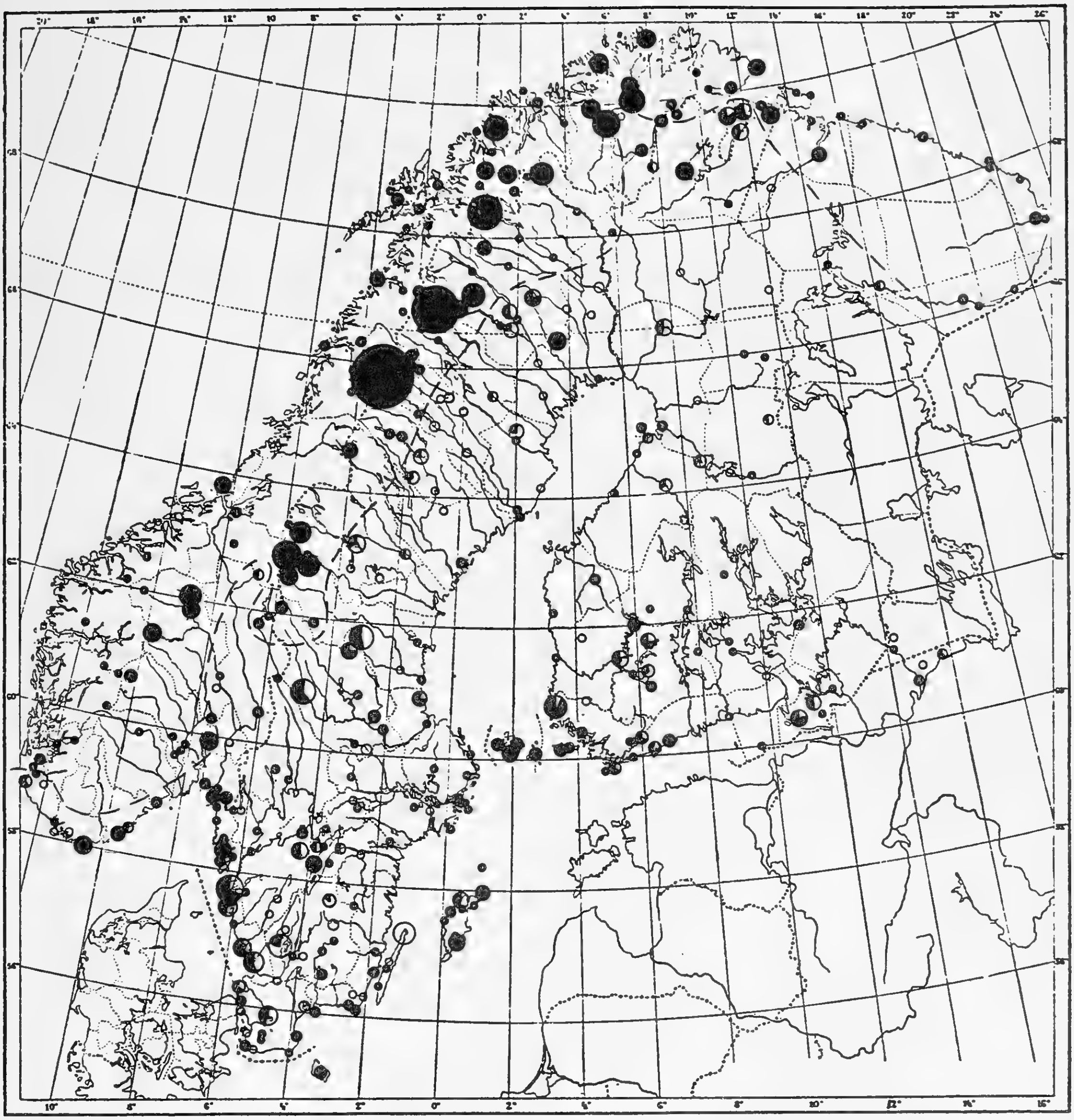


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Fig. 53. *Notiophilus aquaticus.*

Distribution map of wing-dimorphic forms. For explanation see p. 367 and Fig. 28 (p. 368). The broken line indicates the maximum limit of the southern postglacial stock toward the west and north.

was probably equally frequent, since it must not be forgotten that the winds around the high pressure regions above inland ice chiefly move centrifugally, which, with the large differences in altitude in western Norway, resulted in föhn winds (fall winds). These may have favored the fauna and flora of the refuges climatically, but especially temporary higher temperatures have mislead flying insects to swarm flights, as a result of which they got in danger of being carried across the sea. For this reason I believe that *selection in the Ice Age refuges could have caused an elimination of flying insects more than in most of the islands or in the mountains.*

It was stated earlier (p. 338) that the Fennoscandian carabid fauna show a strikingly high percentage of dimorphic species. A closer examination will reveal that dimorphism has been of direct advantage in regions that were repeatedly glaciated during the Quaternary period (see p. 364; cf. also Darlington, 1943, p. 44). During periods of stronger *alterations* (chiefly of climatic nature) the *winged* species and *winged* forms of dimorphic species were clearly favored. Such periods were primarily phases of increase or of melting away of the various glaciations. At the end of each interglacial period the upper
413 existence limits of each animal species were gradually pushed downward and to the south, the biotopes were strongly altered by the fall in temperature, by edaphic alterations (partly catastrophic in nature, such as the summer-like glacial rivers) and impoverishment of species, and finally became uninhabitable for the species concerned. The faster these alterations occurred, the more difficult it became for other than flying individuals to find a suitable new area: *selection operated in favor of macropterism.*

Within the limits of Fennoscandia only such populations escaped destruction which managed to reach regions by a combination of dispersal capacity and chance, that remained ice-free during the maximum of the ensuing glaciation. One might ask if under such circumstances the refuges of the Atlantic coast were reached more frequently only by the winged form of dimorphic species—whether therefore the dimorphism of the species would not have been lost as a result of this escape, and whether brachypterism thereupon must have arisen anew by recurrent mutation within the confines of each refuge. —It is correct that the brachypterous specimens normally must have reached the refuges on foot ("per pedes") since they cannot arise from the homozygous macropterous form without mutation. But during this emigration (which, being chiefly directed *downwards*, would be supported by passive modes of dispersal, such as running water) the possibility existed of *flying* individuals having had a direct positive role in the dispersal of the *brachypterous* form, by reproducing with stray brachypterous specimens in more or less chance unions due to searching for the other sex. From every such pairing a progeny of 50 to 100% brachypterous specimens would have arisen (depending on whether the short-winged or both parents were heterozygous or homozygous). To the extent that fertilized females fly (a question dealt with elsewhere, on pp. 395

and 595), it is possible that a female that has paired with a brachypterous male spreads brachypterism so to speak by air.

In western Scandinavia, with its large altitude differences and consequently with different zones of climate and vegetation closely following one another, the route between the interglacial "place of residence" of the species and the glacial refuge need not have covered many miles. Conversely, we find that even alpine plants (such as *Papaver,* Nordhagen, 1931, 1933) now live in close proximity to the presumed refuges.

During the *glacial periods*, lasting thousands of years, conditions were probably to some extent stable again and selection, as we discussed above,
414 operated in the reverse direction—in favor of brachypterism—to the extent that the hibernating stocks of species, such as *Bembidion aeneum* (p. 399), *Pterostichus strenuus* (p. 395), *Notiophilus aquaticus* (p. 409) apparently (or actually?) became "purely" brachypterous.

The alterations *at the end* of each glaciation may not have been so disastrous as during the growth phase, but the improvement in the climate and the melting of ice sometimes proceeded (for example at the end of the Würm period) very rapidly, so that especially the fauna of open terrain would be threatened to a great extent by forest (see also p. 710). Besides, there were slower but more comprehensive alterations in the distribution of land and water. Hence during this period there were enormous alterations in the biotope which again favored flying animals. This was true, for instance, of the Yoldia period in central Sweden and Finland, and of the Littorina period (and later) in the southern Baltic Sea area, when the problem of overcoming the aquatic barriers arose.

During the more stable *middle* eras of the interglacial epoch the brachypterous individuals were favored by selection, but to a very variable extent, depending on the ecological stenotopy of the species and most strongly (see p. 364) in the case where flying individuals could not easily locate habitable surfaces, and least of all in more or less ecologically ubiquitous species, such as *Bembidion lampros*, *Notiophilus aquaticus* and *N. biguttatus*.

The importance of wing dimorphism for the animals of a repeatedly glaciated area can be summarized as follows: The presence of winged individuals *at the beginning and end* of a glaciation and of wingless individuals during its maximum, reduces the danger of extinction. *By this, the occurrence of dimorphic forms was generally favored in parts of the earth that were glaciated during the Quaternary period.*

A particular problem is whether the present geographical distribution of the two forms of one or other dimorphic carabid species allows drawing any conclusions as to the locality of the Würm refuges. As is well known, such conclusions were drawn by Nordhagen (1933, 1935), generally on phytogeographical grounds, and, following his idea, the presumed refuges are shown on the map of *Bembidion grapei* (Fig. 50).

Most of the dimorphic species that must be considered as west Scandina-
415 vian "winterers", in the west, however, have a continuous, widely distributed brachypterous stock, which provides no further clues in this connection. The following exceptions are noteworthy:

Bembidion grapei, and possibly also *Calathus erratus* indicate a refugium in the Stavanger region.

Bembidion grapei and *B. aeneum* indicate a refugium in Möre (Province 9).

Bembidion grapei and *B. transparens* indicate a refugium in the Lofoten region (33–35).

Bembidion transparens and possibly also *B. grapei* indicate a refugium in Varanger (40–41) or Petsamo.

From an Ice Age refuge must also have originated those dimorphic (and other) species which come from the region around the White Sea by separate immigration, such as *Bembidion aeneum*, *B. guttula*, *B. transparens*, *Pterostichus minor,* and *P. strenuus*, and possibly also *Bembidion nigricorne*, *Carabus clathratus*, and *Pterostichus lepidus*. For the high brachypterism of these stocks must also be due to selection within an isolated region, and the separation from this stock, which (with the exception of *Bembidion aeneum*) colonized the more southerly parts of Finland, would be incomprehensible if they had a common glacial origin at the southeastern edge of the large mass of inland ice.

The question of the glacial overwintering of the fauna is further discussed below in a special section (p. 735 ff.).

416 **Table 29. Distribution of 9 "Würm winterers" among dimorphic carabids within the vegetation zones of the fjelds**

	Regio alpina			*Regio betulina*	*Regio coniferina*
	Higher	Middle	Lower		
Bembidion aeneum	–	–	–	–	+
B. grapei	–	–	+*	+	+
B. guttula	–	–	–	–	+
B. transparens	–	–	–	+	+
Bradycellus collaris	–	–	(+)	+	+
Notiophilus aquaticus	+	+	+	+	+
N. biguttatus	–	–	(+)	+	+
Pterostichus minor	–	–	–	–	+
P. strenuus	–	–	–	–	+

* Outside the region (Siberia, Alaska, Greenland).

The most important result shown by this analysis of the dimorphic carabids of Fennoscandia is that at least 7 species must have survived the last glaciation within the confines of the region, in addition to 2 species (*Bembidion guttula, Pterostichus minor*) probably along the eastern edge, in the vicinity of the White Sea. An ecological study of these species may provide an understanding of the climatic and other conditions in the refuges during the Würm period. It will be interesting at this stage to give the present distribution pattern of these 9 species in the usual vegetation zones ("regions") of the Fennoscandian fjelds (Table 29). This is an excerpt from the larger Table 30 (p. 440).

We conclude that apparently only *Notiophilus aquaticus* can servive under high arctic conditions. In the *Regio alpina* only 4 of the 9 species have been
416 recorded. The occurrence of two of them is more or less accidental and a third does not occur within the Fennoscandian region. Four species have not even been recorded even once in the *Regio betulina*. —These are facts which cannot be reconciled with the traditional concept of Ice Age conditions.

Synthetic Part

The Definition of Area

417 The concept of "area" (Areal[†]; region of distribution) of an animal or plant species is fictitious. What is involved is not a terrain occupied, but a sum of points—individuals—which in the case of animals possess a more or less pronounced totality of mobility. Furthermore, this totality of points cannot be added up all at the same time. The fiction is therefore predicated on space, and also by time.

The zoogeographical term "area", which is nevertheless very useful, is best defined by its limits. These do not delineate more or less homogeneous areas, such as the *forest limit* of the fjelds; these limits are homologous with the *treeline*. An area limit is therefore a line drawn to join up the outermost (northernmost, highest, etc.) localities of an animal or plant species. It would of course be preferable if instead of "localities" we could fall back on populations, definite occurrences, or the like. But as far as insects are concerned, in practice it is possible to decide only in exceptional cases whether the animal found at the sampling region has appeared accidentally or is actually native to that place. The area limits are therefore easily drawn too far out.

The more demanding a species is, the more stenotopic it is, the more disjunct is its area (see examples on p. 563), since most terrains are uninhabitable for it. A hypothetical example of how one can visualize the actual and momentary distribution of a stenotopic insect species within a limited part of its periphery, is provided by the accompanying map (Fig. 54). It may be noted that to the north the species in question selects only the most favorably situated (sun exposed) places, and that individuals that have strayed—including those found in biotopes alien to the species—easily misrepresent the true distribution.

What then are the "area" and "area limits" in the present case? —To me it appears that the answer will vary, in keeping with the task set by the researchers. For the pure ecologist the area of the species can include only the
419 actually, constantly inhabited terrains (marked black in the map). A continu-

[†](Suppl. scient. edit.).

ous area limit is of little actuality for the ecologist. On the other hand, for the zoogeographer, whose chief interest is historical, and who wishes for instance to interpret the postglacial processes of immigration, the above broader (however less exact) use of the term is more practicable, not least since he mostly works with much more extensive regions. He is satisfied with the following definition: *The area limit is a line, up to which the species concerned constantly occurs in suitable terrains.* However, because of enemies, competition with other animals, chance, etc. no species occupies all the terrains suitable for it. On the model map (Fig. 54) the suggested zoogeographical area limit is marked with a crossed line.

The area limits—in the above sense of the word—are not only highly unnatural lines, they are sometimes completely hypothetical. Highly isolated occurrences, be it in advanced outposts or relicts, should be left outside the continuous area limit. Wherever two separate immigrating stocks come close, it is often impossible to decide how to allocate solitary records of the intervening region (for instance Andersson and Birger, 1912, p. 335, *Anemone nemorosa*; Ekman, 1922, p. 201, *Sterna paradisaea*). Such considerations led me to decide not to draw any area limits in the maps given in Part II. However, in the present part the terms "area" and "area limit" are always used in the broad, zoogeographical sense of the word. I believe even critics of these "constructs" do not mind speaking of the northern limit of an animal species.

Finally, it may be mentioned that it seems not unjustified in working with the "area of a species" even where the species has been divided into subspecies, ecotypes, etc. One can even speak of areas of a genus, etc.

The Reliability of Distribution Maps

Occasionally, even being awake, I have a terrible dream. The *real* distribution image of one of my carabid species is presented to me! —However, (unfortunately or fortunately?) we never achieve such an image.

420 There is no avoiding the most important question: How reliable actually are maps published in a book like this one? The answer is best obtained by considering the most important sources of error. These are:

1. *The region in question has been inadequately or in any case erratically explored.* Actually, not even a small terrain is being completely explored, not only because the researcher does not come across everything, but also because the composition of the insect population is subject to continuous alteration. That faunistic or floristic research can never end is all the more true of large regions such as Fennoscandia. Goethe's words, cited by Horion (1941), apply here: "Such work is actually never complete; one has to pronounce it complete." Now, in judging the stage of the map at which this "declaration" may be made, biogeographers apparently hold extremely divergent opinions. I have

418

Fig. 54. Northern peripheral region of the hypothetical, momentary "area" of an insect species bound to shores and banks of a particular type.

Black areas—Populations; Black circle—Single individual; Stippled—Suitable biotopes. The presumed isotherm is "macroclimatic," i.e. obtained by usual meteorological measurements. Crossed line—Zoogeographical "area limit".

(1939, pp. 242–243) already formulated my criteria for the distribution map to be ripe (i.e. for publication):

"... the map must be at least 'credible.' The evidence that this stage has been attained can be tested when any new record can be naturally fitted into the earlier picture without 'destroying' the integrity of the map. If a really surprising locality of a carabid species in Sweden [in the present context: Fennoscandia] has been added only two or three times in recent years, I consider this proof that my carabid maps have almost reached the stage of 'credibility'." Today, nine years later, almost every year other "surprising localities" are added, which cannot all be attributed to late immigration. Nevertheless, I have ventured "to declare the maps ready," i.e. they have been published, not as final documents but as a basis for zoogeographical discussion.

If the general or so to speak the average reliability of the maps is sufficient for this purpose, the often *erratic* exploration of the region must not be overlooked. Some gaps in the distribution can readily be considered artificial. To these, for each species, attention was drawn in Part I. Some of them have subsequently been filled in with additional data provided in the Supple-
422 ment. Assessment of the detailed situation will be facilitated by a map on the frequency of coleopterological exploration of the region (Fig. 55). In 1938, I published such a map for Sweden.

As already mentioned, the decision as to a distribution map being ripe for publication varies greatly with different researchers. As an example of a "premature map" in the Fennoscandian region, mention may be made of the work of Somme (1937) on the zoogeography of Odonata. One is not justified in basing zoogeographical conclusions on distribution maps that are so incomplete. The situation is different when the author himself is aware of the imperfection of his maps and draws no biogeographical conclusions from them, but regards the maps as an impetus for further research. P. Palmgrén (1939, 1943) did this in the case of spiders of Finland and also provided a map on the frequency of exploration of the region (1939, p. 81). But personally I doubt if such maps are deserving publication, having been prepared only for "pedagogic" purposes. All too easily greater significance than is intended can be attributed to them by other researchers, especially foreigners, who have not been apprised of the correct situation and may thus misuse them. A map that is not only the clearest and simplest method of depicting the known distribution of an animal or plant species, it is also a wonderful puzzle of nature, which one wishes to solve at once. It is not very nice to present an "illusory puzzle."

Let us pass over those maps, especially of the Southern Hemisphere, that comprise solitary, widely separated points which have prompted assumptions about land connections in all directions across the oceans. And if one is not sufficiently acquainted with the distribution of the *species*, one can prepare maps of *genera* and families and draw smart conclusions.

2. *The map does not reflect the present and unique state*. The Fennoscandian

421 Fig. 55. Relative exploration of Coleoptera in the Fennoscandian region.

Black—Well explored; Squared—Moderately explored; Hatched—Poorly explored; White—Not explored at all. Assessment, which is subjective, is based on records of Carabidae up to 1947.

carabid maps are the result of nearly 150 years of collecting. During this period the fauna has demonstrably altered in both negative and primarily positive directions, a problem to which a separate section is devoted below (pp. 621 ff.). Some especially clear examples of very recent immigrations are
423 cartographically depicted. Theoretically it would always be more correct to prepare a separate map of the animal species concerned for each epoch (for instance, every decade). In practice that is not feasible, since the number of entomologists is not large enough to bring together material for a nearly complete map. Moreover, there is no date on the labels of any of the older collections of Coleoptera or, (alas!) even of some of the collections still being built up. Finally, in Fennoscandia the faunistic changes of the last century were predominantly of positive nature: New species immigrated, some older ones expanded their area (especially northward and westward). Hence with remarkably few exceptions *the maps provided here reflect the present areas of the species*, of course in the most important features *with regard to the area limits*, if not in detail, since there have been vast changes in the biotopes, especially in the south. In our region the possibility of immigration of transgrading species from all possible directions is not as great as, for instance, in Germany. Hence Horion's repeated exhortations (for example, 1941, p. 5) to note the yearly fluctuations in the faunal stock need be accepted only to a limited extent.

3. *The maps do not record abundance and frequency.* Yet these determine the focal point of the area, and when it lies in a relatively poorly explored region it may even show up as a patch of sparser points compared to better-explored peripheral parts where the animal is not as common. It would be especially interesting to find out whether the species gradually decreases in numbers toward the limit of its area or whether its abundance remains undiminished right up to this boundary, which would help to answer the question whether there is an existence limit or a dynamic limit. Preparation of a map of the desired type is impracticable mostly because of the paucity of material. Frequency or abundance can hardly ever be determined on the basis of the collections, since very few entomologists make the relevant notes in the field.

Miscodera arctica (Fig. 56) has been chosen as a simple example of what such a "quantitative" map might look like. If 1, 2, 3, or more specimens were collected *on the same day*, this has been indicated by four types of circle of different sizes. In spite of the numerous records the pronounced rarity of the species becomes evident in the south and along the coast, and it shows
425 up much more clearly as an animal of the north and the fjelds. Similarly we can illustrate the southward tapering off of a high boreal species, such as *Pterostichus adstrictus*, or the decline of *Amara similata* or *A. aenea* toward the north.

A few words on the best mode of marking a distribution map. I have selected the simplest method: each locality is represented by a point. This is also the most correct method. As soon as illustration by indication, by

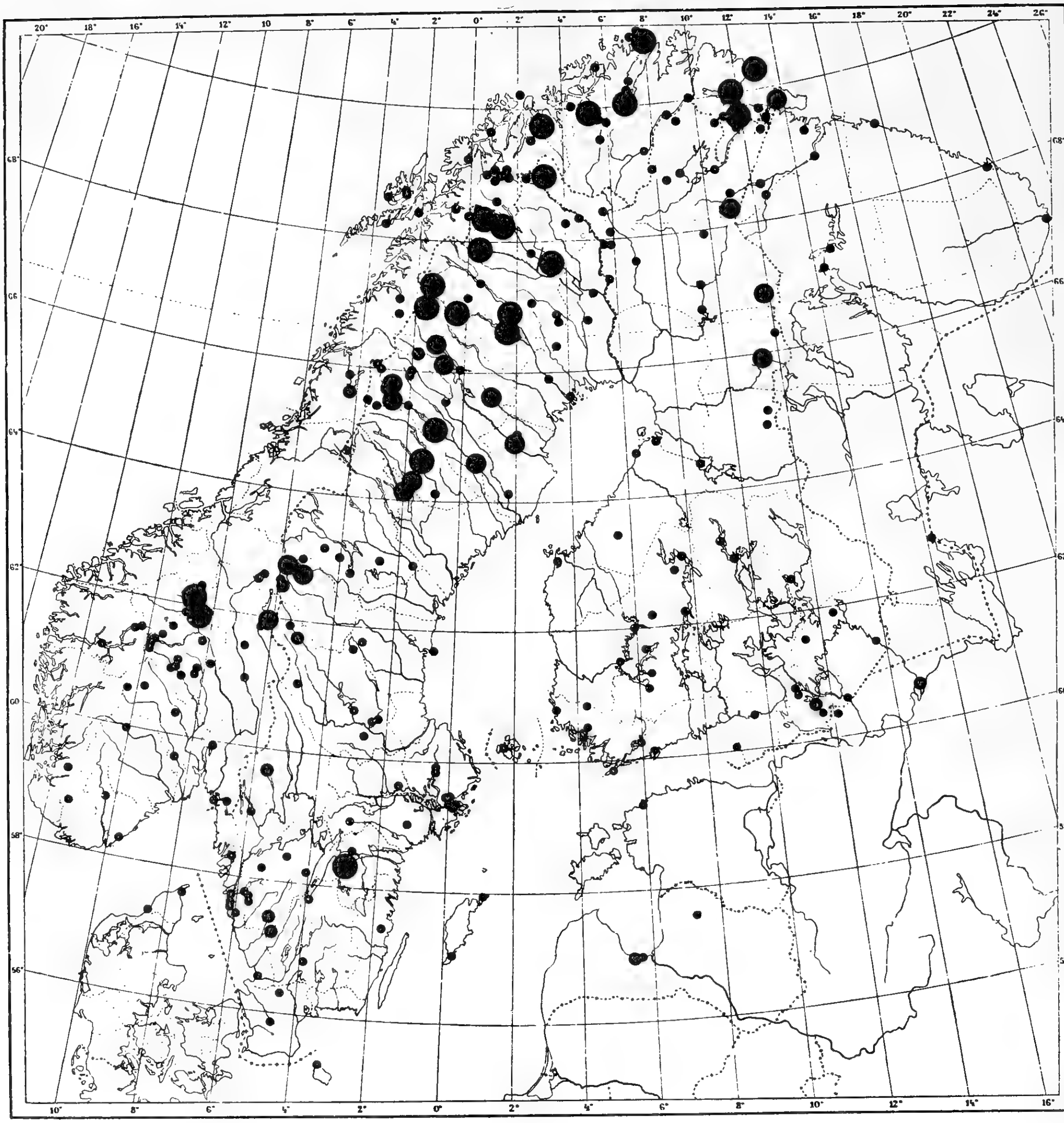

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Fig. 56. *Miscodera arctica.*

"Quantitative" map. Largest circles indicate 4 or more specimens collected in one day, smallest only one specimen (or an unknown number).

hatching, etc. of large regions is used, precision suffers. Examples are the publications of Sainte-Claire Deville (1930a), Holdhaus and Lindroth (1939), etc. The two methods are combined by Sainte-Claire Deville (1930b), Somme (1937) and Hultén in his botanical studies (see below). The "surface method" seems to me justified in cases where a very large region, for instance a whole continent, is mapped. The exact siting of the points has a smaller role and a point-map would give a very unnatural impression, since without exception exploration of large areas has been more or less erratic. Unavoidably, the "surface method" glosses over actual gaps in the distribution, and such maps may easily prompt erroneous conclusions. For even the smallest lacunae of the area, as far as their existence can be actually determined, may be most significant for the history of immigration, many examples of which are provided in the present work. This is also true of plants. The method used by Hultén on a grand scale in his work which is being published on the Fennoscandian distribution of vascular plants, namely, the representation of the area largely by hatched surfaces, is of course understandable. Who would want to map *Calluna vulgaris* by the "point method"? But some important details of the distribution have been lost. In the case of insects, which never extend over large terrains as a continuous "stock," and for which the observation material is still in no case insurveyable, the point method of mapping a region the size of Fennoscandia must be considered in principle as the only reliable method.

But it seems to me important to emphasize that *all* known localities must be marked on the map (as long as they are far enough apart on the particular
426 scale). The procedure adopted by Somme (1937, p. 134: "Where the localities are very close, and not every single record is indicated") is decidedly to be rejected, being an attempt to mask the uneven exploration of the region.

An aberration of the point method, used mostly for economy in printing, is the representation of several species on the same map, using different signs. Striking examples are found in Breuning (1932–36), Heberdey (1939), and Malaise (1945, p. 51), where 8 to 20 (in Breuning up to 60!) species or subspecies are represented together on a single map. This method is understandable where it is intended to illustrate the total distribution of a genus or a group of species. In all other cases it seems to me completely misguided. If I were given the choice of publishing 10 maps of the distribution of 20 species I would prefer to leave out half of them rather than to put 2 species on a common map (with the exception of cases where the two areas are mutually exclusive). The superiority of the picture provided by a map over a list of localities lies in the fact that just one glance gives an understanding of the relative continuity of the area and of the connection between its parts. And, this picture harbors the explanatory attempts. The "collective" maps lack these advantages.

An original approach was adopted by Borchert (1938), who published the

European distribution of all the German beetles in the form of "model maps" of 93 species. Each of the remaining species was referred to one of these "models" in the text, with additions and deletions. Distribution data given in the text in this form are hard to follow, partly because of the abbreviations; otherwise the data seem to have been very carefully gathered from the literature.

This brings us back to the main basic question: Are the distribution maps of the Fennoscandian beetles true to nature to the extent that they could serve as the basis for determining the area-limiting factors and the postglacial history of immigration of these insects? Compared with other distribution maps of insects they are good, but it would be apposite to pose the question: Is it possible for the insect collector—or insect collectors over an entire century—to come
427 across such a large portion of the insects occurring in nature in a region, a province, or an entire country, etc. that the species composition can be judged adequate for a fairly true-to-nature mapping? More simply stated: *How many of the actually existing species does the collector find*?

Eigin Suenson (1934) made an interesting calculation on the number of species of carabids that he collected in Denmark on various excursions. Summarizing the results of his collecting trips, which represent 112 days of collecting (i.e. fairly corresponding to an intensively utilized summer), he recorded a total 191 species, which is 65% of the Danish fauna.

My experience in the summer of 1936 was similar, when I undertook a trip to supplement the carabidological survey of the most poorly studied parts of Sweden (map in Fig. 57). By coincidence, the result, 211 species in 73 days of collecting, constitutes exactly the same component of the Swedish fauna, 65%, as Suenson obtained for Denmark. It may be mentioned that the trip was not undertaken to collect as many species as possible but to complete the distribution map of some particular species, and the number could have been easily increased by short visit to Öland–Gotland or to the fjelds.

Within smaller areas comparisons can be still more advantageous. Suenson (l.c.), in only 9 days of collecting on Bornholm, found 81 carabids (= 36%)* of its fauna. On Gotland in the spring of 1940, in a total of barely 15 days I collected 134 species, constituting no less than 69% of the carabid fauna of this island. The best results of collecting I have ever had for *one* day were in the environs of the city of Mariestad (Vgl) on June 10, 1936. In a region of at the most 5 km^2, along the shore of Lake Vänern, 79 carabid species were collected, i.e. 24% of the entire Swedish fauna and 37% of that of the province of Vgl (214 species).

From the above figures it is clear that an experienced collector who is acquainted with the ecology of every species and restricts himself to a moderately large group of animals can obtain a major part of the fauna in a short

*Perhaps still more, since it seems that he did not take along some of the commonest species.

period of time. The conditions with regard to carabids are especially favorable, since they have a relatively exposed mode of life and a relatively long adult
428 lifespan, so that, with few exceptions, they can be collected during the long period from May through September.

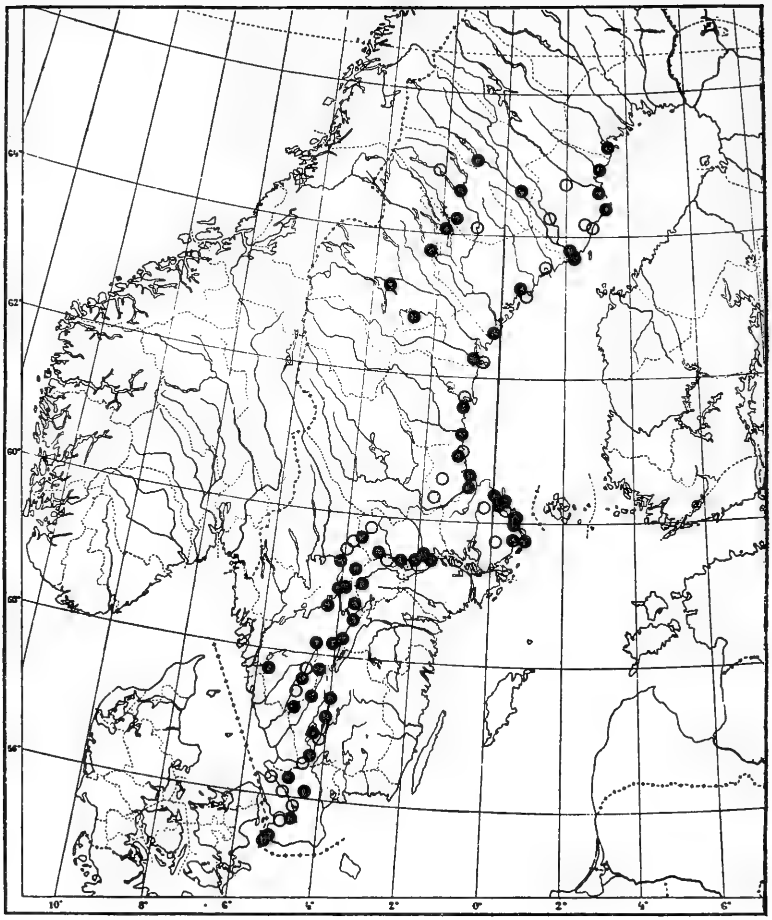
As rightly noted by Suenson (l.c., p. 476) it is the "rare," often biogeographically interesting species (relicts, transgrading species, etc.), that escape attention. But experience shows that the word "rare" can often be replaced
429 by "stenotopic." Once the correct locality of the species has been discovered the "rarities" often reveal an astonishing abundance. An example is *Trechus rivularis*. Distribution types which are distinctly divided in subareas are frequently explicable just because of their restriction to special biotopes. This is especially evident in the shore beetles, which depend on a definite grain size of shore material (for example, *Bembidion*), in burrowing sand beetles (*Harpalus*, etc.), peatbog insects, such as *Agonum ericeti*, etc. (see p. 563).

Of course it may be gladly conceded that some species at the periphery of their area or in their relict areas are *really* rare. *Miscodera*, and more so *Pterostichus adstrictus*, can very easily escape attention in south Sweden, and probably have remained undiscovered in some regions. Records of a transgrading, only accidentally occurring species (i.e. *Agonum gracilipes, Harpalus calceatus* and *H. griseus*) are determined purely by chance; however, in such cases the completeness of the map, even the exact position of each locality is of minor importance.

At the outset some facts were mentioned in support of the view that the maps presented in this work are to a great extent true to nature. In support of this we may cite:

1. *The frequency of remarkably regular lay of the northern limit* of a number of southern species, for instance *Agonum obscurum*, *Broscus*, *Pterostichus vulgaris*. Likewise the Swedish eastern limit and the Finnish western limit respectively of *Carabus concellatus* and *Cicindela hybrida*. Even inconspicuous carabids like *Bembidion illigeri* and *Trechus secalis*, which have not been collected by every entomologist, show sharply defined area limits.

2. *The extremely rare discovery in recent decades of any new carabid species in Sweden*. Altogether 20 species (6.8% of the fauna) have been collected for the first time in Sweden during this century. Of these only 3 have been collected during the last 10 years (1938–1947). In the context of changes in the fauna (pp. 621 ff.) these "new arrivals" are studied in more detail. This study shows that 6 (possibly 10) of the above-mentioned 22 species must have actually immigrated to Sweden very recently. Of the remaining species, 5 were found exclusively and 6 others at least predominantly at localities, such as the Abisko region, that were not visited by entomologists before 1900. Three others are márkedly stenotopic species (*Agonum munsteri*, *Perileptus*, *Tachys bisulcatus*),
430 whose discovery almost presupposes a knowledge of their concealed mode of life. Only 4 species are left, *Carabus intricatus*, *Dromius longiceps*, *Dyschirius*



428 Fig. 57. Author's collecting localities in 1936 (May 28 through August 15). Blank circles indicate superficially explored localities; Black circles more carefully investigated ones.

septentrionum and *Harpalus rupicola* (if the last of these has not recently immigrated), that escaped the notice of earlier entomologists. However, this actually forms a very small component of a fauna of 326 species. In expressing our admiration for the earlier collectors, like Gyllenhal, Zetterstedt, Boheman, or Thomson, we must recognize this as evidence for the remarkable completeness

of the results of their entomological collecting activity.

Conversely we are also justified in considering carabids such as *Agonum bogemanni* or *Harpalus nigritarsis*, which have not been found in Sweden in this century, as vanishing or even extinct species.

What has been said for Sweden applies to Finland almost to the same extent. On the other hand, Norway has been irrefutably less explored. It is thus to be expected that future noteworthy changes in the picture of the Fennoscandian distribution map of one or other species will take place mainly in that country.

The Relationships of the Fennoscandian Fauna

Only two carabids, *Bembidion scandicum* and *Bradycellus ponderosus*, are known exclusively from Fennoscandia, and are therefore (provisionally) to be considered as endemic to the area. In all other cases it is clear that only a precise knowledge of the *total area* of the species concerned can provide sufficient clues to its history, for example on the dynamic center.

Distribution maps of the total area, at least of the most interesting species, would thus be highly desirable. I have simply not *ventured* to undertake the preparation of such maps. When the sources of error are already so large in a relatively small region like Fennoscandia, and the need to verify all the records published and unpublished imperative, the preparation of such maps of the total area must be considered unattainable, even for a limited number of species. I have been impelled to exercise the utmost caution with regard to the locality data in the literature, following the sound critical approach laid down by Horion (1941, Preface).

Attention has already been drawn in Part I of this work (and in the Supple-
431 ment at the end of this part) to the maps already to be found in the literature on the total area of one or other carabid species. The maps by Sainte-Claire Deville, and the maps of *Bembidion* by Netolitzky, seem to be the most reliable.

In Part I, with every species a characteristic of the distribution type was given. This was done partly with "code words" (circumpolar, palearctic, etc.; see Part I, p. 13). But it must be emphasized that these terms are valid so to speak "proceeding from Fennoscandia" and comprise—especially the term "palearctic"—species with very different total areas. A more natural division into immigration groups will be considered below (p. 703).

Nevertheless it might be useful to summarize the Fennoscandian fauna according to the above "group designations." This gives us the following results:

Circumpolar species (in Europe, Asia, and North America):	26
Palearctic species (in Asia, at least to longitude 60° E):	225

West Palearctic species (in Asia, as far as West Turkestan):	46
Euro-Caucasian species (possibly also in North Africa):	11
Euro-Mediterranean species (in North Africa and (or) the Near East):	10
Purely European species (also missing from Caucasus):	42
Amphi-Atlantic species (in Europe, the Mediterranean region and North America):	2

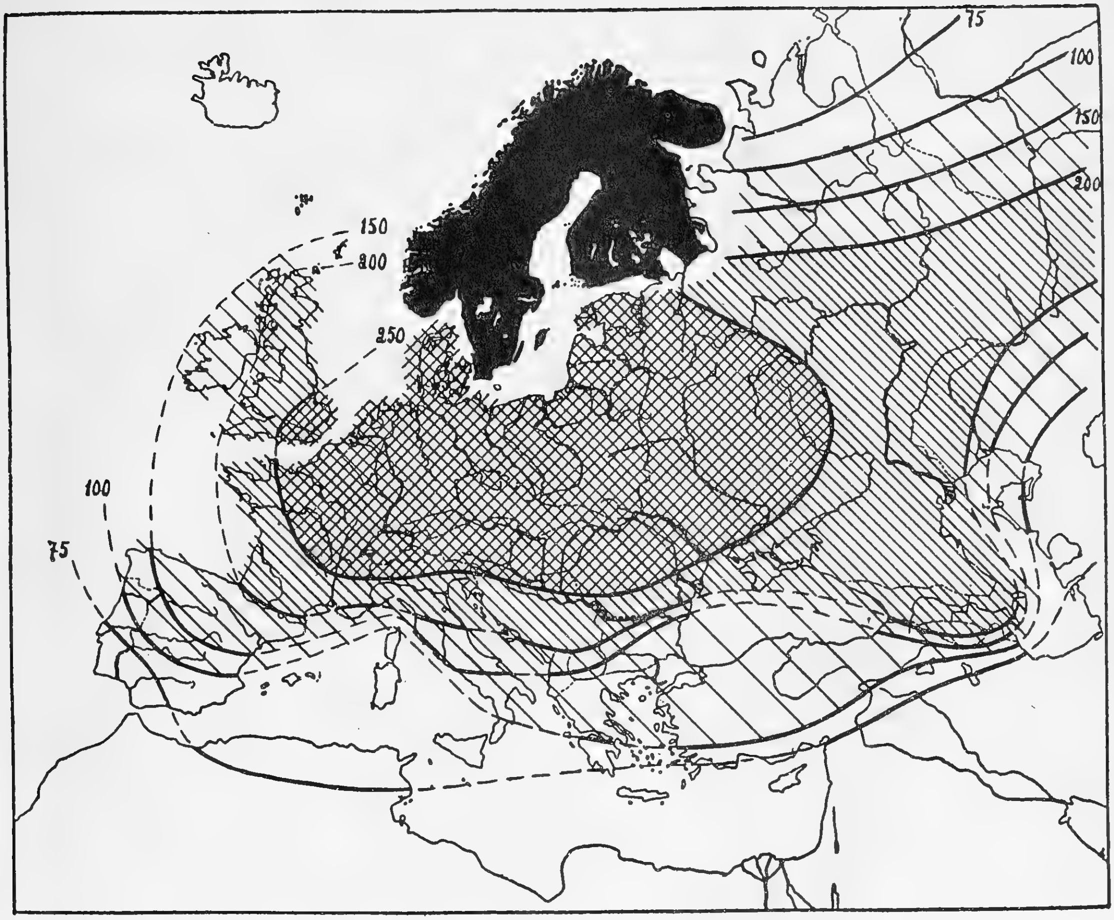
A better general view is provided by a cartographic representation of the number of species that Fennoscandia has in common with various subareas (Figs. 58, and 59). Since these figures vary widely in accordance with the size of the selected region for comparison, and evidently depend on the more or less thorough exploration thereof, they offer no absolute value, but give a definite impression of the extent of the faunistic relationship.

The first thing that strikes one is the vast, in most cases, probably continuous distribution of our species to the east, with about one-half of the Fennoscandian fauna having been found even in central Siberia. The high numbers in North Asia are all the more striking, considering that in East Fennoscandia there are only 298 species compared with 326 in Sweden (Norway has 244 species, and little Denmark has 308 species). The distribution of the species within the confines of Fennoscandia (Fig. 60) also shows that south Sweden has incomparably the richest fauna, suggesting a relationship "directed" predominantly toward the south.

432 Especially instructive is an analysis of the above stereotyped 7 patterns of distribution types according to the dynamic characteristics of their compo-
433 nents (Fig. 47). The "Euro-Caucasian" and "Euro-Mediterranean" species are appropriately combined and the two "amphi-Atlantic" species are ignored. As usual, a distinction has been made between *macropterous, brachypterous and*
434 *dimorphic* species: all the carabids showing wing-dimorphism in some part of their area have been placed in the last group.

435 Diagram 47 unmistakably shows that the species with especially restricted distribution—the "purely European" species—are largely flightless. The percentage of macropterous species increases gradually and steadily with the size of the area and attains its highest value (85%) among the circumpolar species. It is also interesting to note the intermediate position of dimorphic species, which form the largest component among species having *moderately* wide distribution (groups b and c).

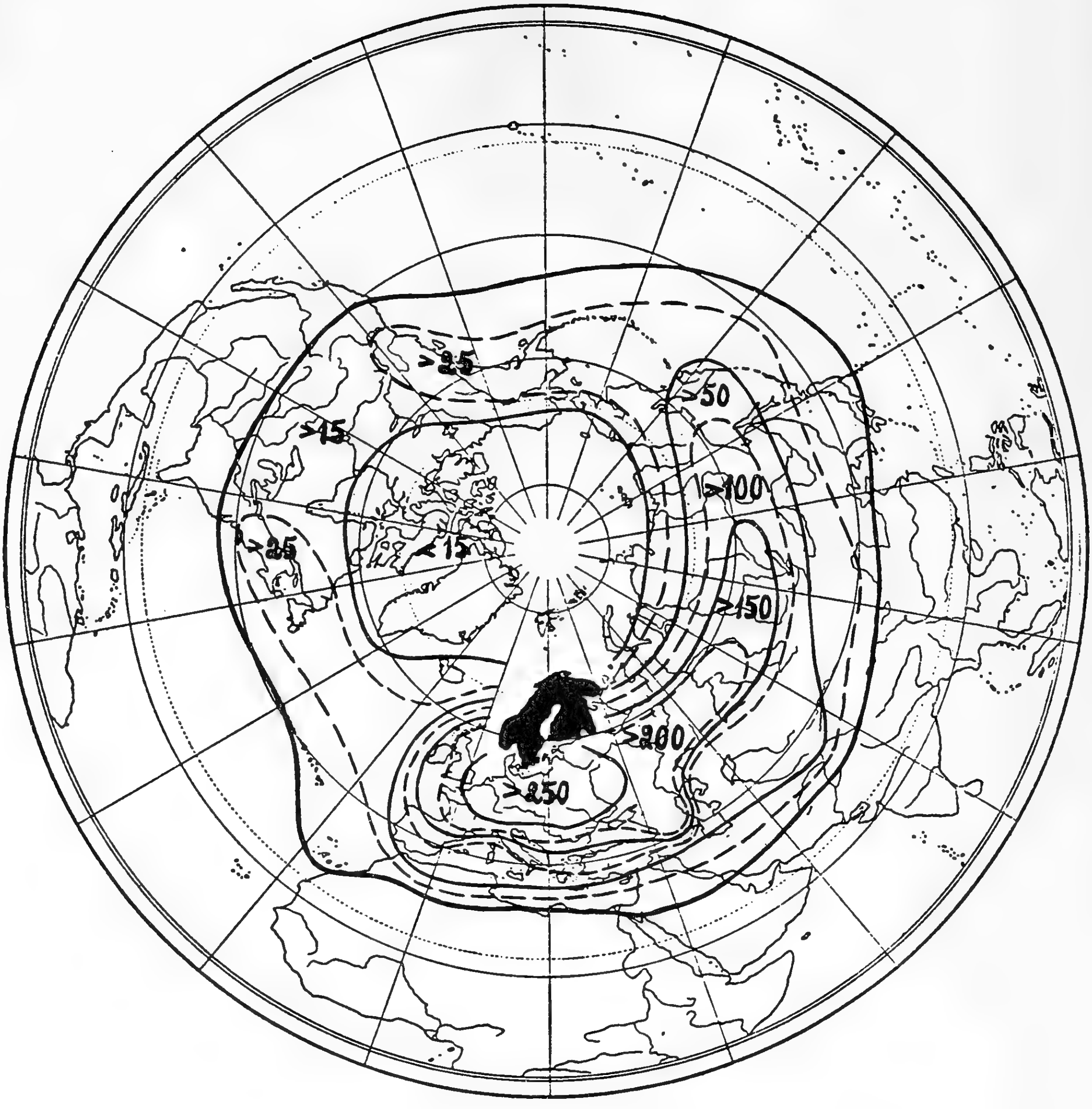
A word of caution against possible misinterpretation of the two maps (Figs. 58, 59) is that these tend to give the impression of Fennoscandia as a center, from which the species emigrated in different directions for different distances, depending on their dynamic characteristics. Nothing could be more incorrect. In the total area of individual species, Fennoscandia usually occupies a peripheral position; for a smaller portion of the entire population of a species the region may have been important at the most as a *secondary* center (during



432 Fig. 58. Approximate distribution of 362 Fennoscandian Carabidae in the rest of Europe.

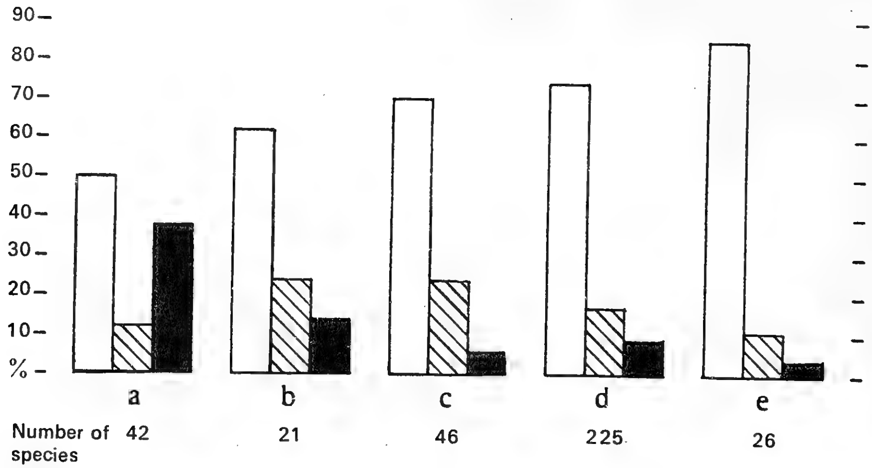
the Würm Ice Age).

436 The method of collective mapping of species with more or less similar distribution according to the "theory of equiformal progressive areas" (Hultén, 1937) also poses the danger of overestimating the role of the selected starting region as a distribution center. Hultén, who studied the distribution of higher plants, failed to avert this danger. In line with his choice of the starting region, he clearly overestimated northeastern Asia as the original center (Holdhaus and Lindroth, 1939, p. 273).



433 Fig. 59. Approximate world distribution of the 362 Fennoscandian Carabidae.

434 Fig. 60. Approximate number of carabid species in different parts of Fennoscandia.



435 Diagram 47. Percentage composition of macropterous (blank), dimorphic (hatched), and brachypterous (black) species of Fennoscandian carabid fauna within different distribution groups.

a—Purely European species; b—Euro-Caucasian and Euro-Mediterranean species; c—West Palearctic species; d—Palearctic species; e—Circumpolar species.

436 **Species Distribution among Different Plant Regions**

For the reasons given above (pp. 43 ff.) no distribution of the Fennoscandian carabid fauna by region was undertaken. On the other hand, it might be valuable to determine the distribution of each species according to the various Fennoscandian vegetation zones, which are especially sharply delimited to the fjeld† areas, where they appear as high-altitude zones. This is the simplest way of estimating the climatic requirement (chiefly thermic) of a beetle. These results can be very useful in judging the climatic and biogeographical influence of the "Ice Age."

The division utilized here represents a simplification of that undertaken by the Swedish botanists. Seven regions are distinguished (cf. map in Fig. 61):

†(Barrier plateau of the Scandinavian upland; suppl. scient. edit.).

437 Fig. 61. Simple division of Fennoscandia into forest regions.

Slant-hatched—*Regio fagina*; vertical-hatched—*Regio quercina*; White—*Regio coniferina* (and *Regio betulina*); Stippled—*Regio alpina*.

Northern coniferous limit is drawn only in east Fennoscandia. Isolated northernmost coniferous forest stands are shown in black. Arrows indicate wooded passes through the Scandinavian watershed; those in *Regio betulina* are indicated by blank circles, those in *Regio coniferina* by black circles. (Ekman, 1922, p. 363; Enquist, 1933)*. After Kihlman (1890); *Atlas öfver Finland*, 1910; Du Rietz (1925, 1935); Enquist (1933); Hjelmqvist (1940).

*The pass in Pite-lappmark, north of the Arctic Circle, is referred to as wooded only by Enquist (1933). It is missing from the map by Hård (1939).

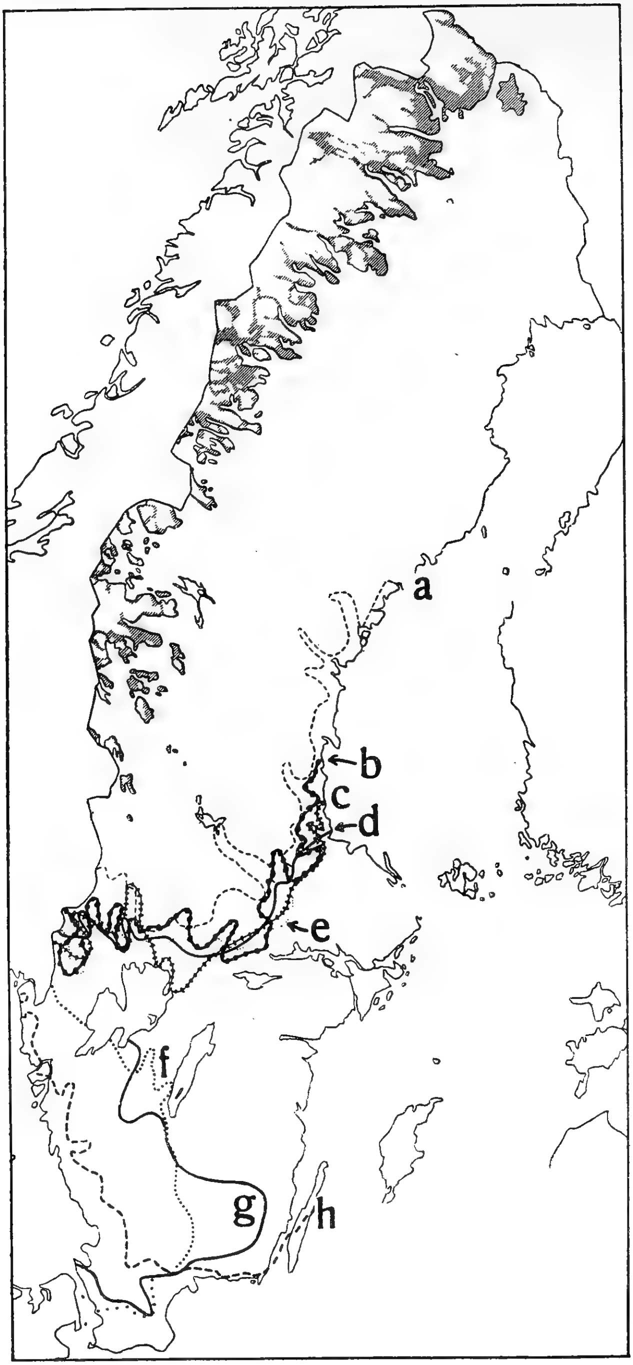


Fig. 62. Vegetation regions of Sweden (according to Du Rietz, 1935a; Hård, 1924).

a—Absolute limit of *Corylus*; b—Absolute limit of *Fraxinus*; c—Absolute limit of *Quercus*; d—Limit of abundant *Corylus*; e—Southern limit of abundant *Betula nana*; f—Eastern limit of abundant *Erica tetralix*; g—Absolute eastern limit of *Narthecium*; h—Southern and western limits of spontaneous *Picea*.

1. *Regio alpina superior* (Higher alpine region†). No continuous vegetation cover of vascular plants. Lichens and mosses dominate (Du Rietz, 1930, p. 358; 1942, p. 184).

2. *Regio alpina media* (Middle alpine region†). In Fennoscandia characterized chiefly by heaths with *Carex rigida—Juncus trifidus*, in the north also with *Cassiope tetragona* (Du Rietz, l.c., p. 357 and p. 183).

3. *Regio alpina* inferior (Lower alpine region†). Dwarf shrub heaths rich in species dominate (in the south with *Calluna*). Sometimes with *Salix* bushes (determined by edaphic conditions), for which reason an "osier region" was proposed (for example, Ekman, 1922, p. 549; 1944, p. 20). Luxuriant meadows on good soil, for instance with *Trollius*, *Geranium silvaticum* (Brundin, 1934, p. 85 ff.).

4. *Regio betulina*. The upper limit (or the northern limit) is formed by the *timber line*, but not by the treeline.

5. *Regio coniferina*. The upper (or northern) limit is the coniferous forest
439 line formed by *Pinus* or *Picea*. Solitary coniferous trees or small groups of them may also occur in the *Regio betulina*.

6. *Regio quercina*. The northern (eastern in West Norway) limit is formed by the absolute northern or the high-altitude limit of *Quercus*.

7. *Regio fagina*. The region with abundant occurrence of stand-forming *Fagus silvatica* (according to Hjelmqvist, 1940).

The division of the *Regio quercina* of south Sweden, generally adopted by botanists, into a western and an eastern part (p. 45) is ignored here because it is hardly climate-based. The position of these and other botanical lines of division, corresponding chiefly with the southern limit of the *Regio coniferina*, is illustrated in the map (Fig. 62).

Let us discuss the most appropriate definition of the southern limit of the *Regio coniferina*, the "*limes norrlandicus*," which has been recently studied by M. Fries (1948). According to him this limit follows a course that reflects the geographical as well as the climatic and biological viewpoints. But the choice of the absolute northern limit of *Quercus* is actually rather arbitary.

In the following Table, which lists all the Fennoscandian carabids, occurrence of the species outside the area is, as far as possible, also taken into consideration. Data exclusively based on such occurrence are given in square brackets. The tundra species are allocated only approximately, according to their advance toward the north. Occurrence in the northern peripheral area of the taiga is noted for the *Regio betulina*. Records in the north Norwegian coastal area, northerly to 70°20′N and easterly to Porsanger, are allocated to the *Regio coniferina*.

†(suppl. scient. edit.).

440–448 **Table 30. Distribution of Fennoscandian Carabidae within the different vegetation zones. Cf. map in Fig. 61.**

Round brackets indicate marginal cases or ± occasional occurrences (apparent cases of wind transport—for instance, in snowdrifts at high localities—are ignored). Square brackets indicate records outside of the region

		Regio alpina		*Regio*	*Regio*	*Regio*	*Regio*
	Higher	Middle	Lower	*betulina*	*coniferina*	*quercina*	*fagina*
Abax ater						(+)	+
Acupalpus consputus						+	+
A. dorsalis					+	+	+
A. dubius							+
A. exiguus					(+)	+	+
A. flavicollis					+	+	+
A. meridianus					(+)	+	+
Aëpus marinus					(+)	+	[+]
Agonum aldanicum			+	[+]	[?]		
A. archangelicum				[+]	+		
A. assimile					+	+	+
A. bogemanni					+	+	
A. consimile			+	+	(+)		
A. dolens					+	+	+
A. dorsale						+	+
A. ericeti					+	+	+
A. fuliginosum			(+)	+	+	+	+
A. gracile			(+)	(+)	+	+	+
A. gracilipes					(+)	(+)	+
A. impressum					+	+	+
A. krynicki						+	+
A. livens					+	+	+
A. longiventre					[+]	+	[+]
A. lugens						+	+
A. mannerheimi					+	(+)	
A. marginatum						+	+
A. micans					+	+	+
A. moestum						+	+
A. mülleri					+	+	+
A. munsteri					+	+	[+]
A. obscurum					+	+	+
A. piceum					+	+	+
A. quadripunctatum					+	+	+
A. ruficorne					(+)	+	+
A. sexpunctatum					+	+	+

	Regio alpina			Regio	Regio	Regio	Regio
	Higher	Middle	Lower	*betulina*	*coniferina*	*quercina*	*fagina*
Agonum thoreyi					+	+	+
A. versutum					+	+	+
A. viduum					+	+	+
Amara aenea					+	+	+
A. alpina	+	+	+	+	(+)		
A. apricaria			(+)	+	+	+	+
A. aulica				[+]	+	+	+
A. bifrons					+	+	+
A. brunnea		(+)	+	+	+	+	+
A. communis					+	+	+
A. consularis					+	+	+
A. convexiuscula						+	+
A. crenata							[+]
A. cursitans					(+)	+	+
A. curta					+	+	+
A. equestris					+	+	+
A. erratica		[+]	+	+	+		
A. eurynota				(+)	+	+	+
A. famelica					+	+	+
A. familiaris					+	+	+
A. fulva					+	+	+
A. fusca							+
A. infima					+	+	+
A. ingenua					+	+	+
A. interstitialis				+	+	(+)	
A. littorea				(+)	+	+	+
A. lucida						+	+
A. lunicollis			(+)	(+)	+	+	+
A. majuscula					+	+	+
A. montivaga					+	+	[+]
A. municipalis			(+)	?	+	+	+
A. nigricornis			+	+	+		
A. nitida					+	+	+
A. ovata					+	+	+
A. peregrina			(+)	[?]	[+]		
A. plebeja					+	+	+
A. prætermissa			+	+	+	+	+
A. quenseli		+	+	+	+	+	+
A. similata					+	+	+
A. spreta					(+)	+	+
A. tibialis					+	+	+
A. torrida			(+)	+	+		
Anisodactylus binotatus					+	+	+
A. nemorivagus					(+)	+	+
A. poeciloides							+
Asaphidion flavipes					+	+	+

	Regio alpina			Regio betulina	Regio coniferina	Regio quercina	Regio fagina
	Higher	Middle	Lower				
Asaphidion pallipes			[+]	+	+	+	+
Badister bipustulatus					+	+	+
B. dilatatus					(+)	+	+
B. peltatus					+	+	+
B. sodalis					(+)	+	+
B. unipustulatus						+	+
Bembidion aeneum					+	+	+
B. andreae polonicum					(+)	+	+
B. argenteolum					+	+	[+]
B. articulatum					(+)	+	+
B. assimile						+	+
B. azurescens					(+)	+	[+]
B. biguttatum					(+)	+	+
B. bipunctatum			+	+	+	+	+
B. chaudoiri					+	[?]	[?]
B. clarki						+	+
B. crenulatum			(+)	?	[?]		
B. dauricum			+	+	[?]		
B. dentellum					+	+	+
B. difficile			+	+	+		
B. doris					+	+	+
B. fellmanni		+	+	+	(+)		
B. femoratum			[+]	(+)	+	+	+
B. fumigatum							+
B. gilvipes					+	+	+
B. grapei			[+]	+	+	(+)	
B. grapeioides			+	+			
B. guttula					+	+	+
B. harpaloides						+	[+]
B. hasti		+	+	+	(+)		
B. hirmocoelum					+		
B. humerale					+	+	+
B. hyperboraeorum			+	+	(+)		
B. illigeri						+	+
B. lampros					+	+	+
B. lapponicum			[+]	+	(+)		
B. litorale				(+)	+	+	+
B. lunatum					+	+	+
B. lunulatum						(+)	+
B. minimum					+	+	+
B. monticola					+	+	+
B. nigricorne					+	+	+
B. nitidulum				+	+	+	+
B. obliquum				(+)	+	+	+
B. obtusum						+	+
B. octomaculatum						(+)	+

	Regio alpina Higher	Middle	Lower	Regio betulina	Regio coniferina	Regio quercina	Regio fagina
Bembidion pallidipenne						+	+
B. prasinum			(+)	+	+		
B. properans					+	+	+
B. punctulatum					+	+	[+]
B. pygmaeum					+	+	[+]
B. quadrimaculatum					+	+	+
B. quinquestriatum						+	+
B. repandum				[+]	+	[+]	[+]
B. ruficolle					+	+	+
B. rupestre			(+)	+	+	+	+
B. saxatile				(+)	+	+	+
B. scandicum				+	?		
B. schüppeli				(+)	+	+	+
B. semipunctatum					+	+	+
B. siebkei				+	+		
B. stephensi					(+)	+	+
B. striatum					(+)	(+)	[+]
B. tibiale					[+]	+	
B. tinctum				(+)	+		
B. transparens				+	+	+	(+)
B. unicolor					+	+	+
B. ustulatum					+	+	+
B. varium					(+)	+	+
B. velox				(+)	+	+	[+]
B. virens			(+)	+	+	+	
Blethisa multipunctata				(+)	+	+	+
Brachynus crepitans						+	+
Bradycellus collaris			(+)	+	+	+	+
B. csikii							+
B. harpalinus						+	+
B. ponderosus					(+)		
B. similis					+	+	+
B. verbasci							+
Broscus cephalotes					+	+	+
Calathus ambiguus						+	+
C. erratus					+	+	+
C. fuscipes					(+)	+	+
C. melanocephalus			+	+	+	+	+
C. micropterus				+	+	+	+
C. mollis						+	+
C. piceus							+
Calosoma auropunctatum						(+)	+
C. denticolle						(+)	[+]
C. inquisitor						+	+
C. investigator						(+)	[+]
C. reticulatum						+	[+]

	Regio alpina Higher	Middle	Lower	Regio betulina	Regio coniferina	Regio quercina	Regio fagina
Calosoma sycophanta						(+)	(+)
Carabus arvensis					+	+	+
C. auratus						(+)	[+]
C. cancellatus					+	+	+
C. clathratus					+	+	+
C. convexus						+	+
C. coriaceus					+	+	+
C. glabratus		+	+	+	+	+	+
C. granulatus					+	+	+
C. hortensis					+	+	+
C. intricatus							+
C. menetriesi					(+)	+	
C. monilis						(+)	[+]
C. nemoralis					+	+	+
C. nitens			+	+	+	+	+
C. problematicus		+	+	+	+	+	+
C. violaceus		(+)	+	+	+	+	+
Chlaenius costulatus					(+)	[+]	[+]
C. nigricornis					+	+	+
C. quadrisulcatus						+	+
C. sulcicollis						(+)	+
C. tristis					(+)	+	+
C. vestitus							+
Cicindela campestris					+	+	+
C. hybrida					+	+	+
C. maritima				?	+	+	+
C. silvatica				(+)	+	+	+
Clivina collaris						(+)	[+]
C. fossor			+	+	+	+	+
Cychrus caraboides			+	+	+	+	+
Cymindis angularis					+	+	+
C. humeralis						+	+
C. macularis					+	+	+
C. vaporariorum		+	+	+	+	+	+
Demetrias imperialis						+	[+]
D. monostigma						(+)	+
Diachila arctica			+	+	+		
D. polita			+	[+]			
Dichirotrichus pubescens			+	+	+	+	+
D. rufithorax					+	+	[+]
Dolichus halensis							+
Dromius agilis				+	+	+	+
D. angustus						+	+
D. fenestratus					+	+	+
D. linearis					(+)	+	+
D. longiceps					(+)	+	+

	Regio alpina			Regio	Regio	Regio	Regio
	Higher	Middle	Lower	betulina	coniferina	quercina	fagina
Dromius marginellus					+	+	+
D. melanocephalus							+
D. nigriventris						+	+
D. quadraticollis					[+]	(+)	[+]
D. quadrimaculatus					(+)	+	+
D. quadrinotatus					(+)	+	+
D. sigma					+	+	+
Dyschirius aeneus					(+)	+	+
D. angustatus					+	[+]	+
D. chalceus						(+)	+
D. globosus			+	+	+	+	+
D. helléni			[+]	+	+		
D. impunctipennis					(+)	+	+
D. intermedius					(+)	+	+
D. lüdersi					+	+	+
D. neresheimeri						(+)	[+]
D. nitidus					(+)	+	[+]
D. obscurus					+	+	+
D. politus					+	+	+
D. „rufipes"					(+)	(+)	
D. salinus						+	+
D. septentrionum			[+]	+	+	+	
D. thoracicus					+	+	+
Elaphrus angusticollis					+	[+]	
E. cupreus			(+)	+	+	+	+
E. lapponicus			+	+	+	[+]	
E. riparius			+	+	+	+	+
E. uliginosus					+	+	+
Harpalus aeneus					+	+	+
H. anxius					(+)	+	+
H. azureus						+	[+]
H. calceatus					(+)	(+)	+
H. distinguendus					+	+	+
H. frölichi						(+)	+
H. fuliginosus			(+)	+	+	+	+
H. griseus					(+)	(+)	+
H. hirtipes						+	+
H. latus			(+)	(+)	+	+	+
H. luteicornis					+	+	+
H. melancholicus						+	+
H. melleti						+	+
H. neglectus						+	+
H. nigritarsis					?		
H. picipennis						(+)	+
H. pubescens					+	+	+
H. punctatulus					(+)	+	[+]

	Regio alpina Higher	Middle	Lower	Regio betulina	Regio coniferina	Regio quercina	Regio fagina
Harpalus puncticeps						(+)	+
H. puncticollis					+	+	+
H. quadripunctatus				+	+	+	+
H. rubripes					+	+	+
H. rufitarsis						+	+
H. rufus						(+)	(+)
H. rupicola						+	[+]
H. seladon					+	+	+
H. serripes						+	+
H. servus						(+)	+
H. smaragdinus					+	+	+
H. tardus					+	+	+
H. vernalis						+	+
H. winkleri			+	+	+	+	+
Lebia chlorocephala					+	+	+
L. crux-minor					+	+	+
L. cyanocephala					(+)	+	+
Leistus ferrugineus				+	+	+	+
L. rufescens				+	+	+	+
L. rufomarginatus						(+)	+
Licinus depressus						+	+
Lionychus quadrillum						(+)	[+]
Loricera pilicornis			(+)	+	+	+	+
Masoreus wetterhalli						+	+
Metabletus foveatus					(+)	+	+
M. truncatellus					+	+	+
Microlestes maurus					(+)	+	+
M. minutulus					+	+	+
Miscodera arctica		+	+	+	+	+	(+)
Nebria brevicollis						+	+
N. gyllenhali	(+)	+	+	+	+	+	
N. livida					+	+	+
N. nivalis	+	+	+	(+)			
N. salina					(+)	+	+
Notiophilus aquaticus	+	+	+	+	+	+	+
N. biguttatus			(+)	+	+	+	+
N. germinyi			+	+	+	+	+
N. palustris					+	+	+
N. pusillus					(+)	+	+
N. reitteri			(+)	+	+		
N. rufipes							+
Odacantha melanura					(+)	+	+
Olisthopus rotundatus					+	+	+
Omophron limbatum						+	+
Oodes gracilis						+	[+]
O. helopioides					+	+	+

	Regio alpina Higher	Middle	Lower	Regio betulina	Regio coniferina	Regio quercina	Regio fagina
Panagaeus bipustulatus					(+)	+	+
P. crux-major					+	+	+
Patrobus assimilis			+	+	+	+	+
P. atrorufus				+	+	+	+
P. septentrionis	+	+	+	+	+		
P. sept. australis					+	[+]	[+]
Pelophila borealis		(+)	+	+	+	(+)	
Perileptus areolatus					+	+	[+]
Pogonus luridipennis						+	[+]
Pristonychus terricola						+	+
Pterostichus adstrictus				+	+	(+)	
P. aethiops					(+)	+	[+]
P. angustatus					(+)	+	+
P. anthracinus						+	+
P. aterrimus					(+)	+	+
P. coerulescens					+	+	+
P. cupreus					+	+	+
P. diligens			+	+	+	+	+
P. fastidiosus			+	[+]	[+]		
P. gracilis					(+)	+	+
P. lepidus					+	+	+
P. madidus						(+)	[+]
P. middendorffi			+	[+]	[+]		
P. minor					+	+	+
P. niger					+	+	+
P. nigrita			(+)	?	+	+	+
P. oblongopunctatus				(+)	+	+	+
P. punctulatus						(+)	+
P. strenuus					+	+	+
P. vernalis					+	+	+
P. vulgaris					+	+	+
Sphodrus leucophthalmus					+	+	+
Stenolophus mixtus					(+)	+	+
S. teutonus							+
Stomis pumicatus					(+)	+	+
Synuchus nivalis					+	+	+
Tachys bistriatus					(+)	[+]	[+]
T. bisulcatus					+	+	[+]
Tachyta nana				(+)	+	+	(+)
Trachypachys zetterstedti				?	+	[+]	
Trechus discus					(+)	+	+
T. fulvus					(+)	+	[+]
T. micros					(+)	+	+
T. obtusus			(+)	+	+	+	+
T. quadristriatus					+	+	+
T. rivularis					+	+	+

	Regio alpina Higher	Middle	Lower	Regio betulina	Regio coniferina	Regio quercina	Regio fagina
Trechus rubens					+	+	+
T. secalis					+	+	+
Trichocellus cognatus			+	+	+	+	+
T. mannerheimi			+	[+]	[+]		
T. placidus					+	+	+
Zabrus tenebrioides							+

448 Summation gives the following figures for each of the seven regions:

Higher *regio alpina*:	4 + (1)	hence	5 species (max.)
Middle *regio alpina*:	12 + (3) + [1]	hence	16 species (max.)
Lower *regio alpina*:	43 + (20) + [9]	hence	72 species (max.)
Regio betulina	67 + (17) + [8] + 6	hence	99 species (max.)
Regio coniferina	206 + (58) + [6] + 6	hence	276 species (max.)
Regio quercina	273 + (34) + [8] + 1	hence	316 species (max.)
Regio fagina	272 + (5) + [38] + 1	hence	316 species (max.)

This summary highlights the extreme paucity of the carabid fauna in high alpine Fennoscandia. The only species exclusively native to the *Regio alpina* is *Nebria nivalis*.

Earlier I gave a survey of all the Coleoptera known at that time from the Swedish *Regio alpina* (Lindroth, 1935b, pp. 25 ff.).

Existence Factors

Climate

449 Generally—and probably correctly—*climatic* factors have been considered decisive in determining the area limits of an animal or plant species. This is certainly valid as long as we study the main features of the distribution of animals and plants from the Equator toward the poles, or when we take into consideration larger regions, such as the African continent, which have remained more or less unaltered through long geological epochs. On the other hand it might be more than dubious to consider the fauna of a newly originated island as determined mainly by the climate. An intermediate position is occupied by regions which, like Fennoscandia, were colonized only in a geologically late period, chiefly in the postglacial period.

According to the definition of the term "climate" it is important to determine not only its characteristic as the *average* condition of the atmosphere during any given number of years but also the spatial validity of the measurements taken. As a rule it is true that the higher the recording apparatus is placed above ground level, the greater the area (at the same height) for which the representative values are obtained. Thermic and most other meteorological instruments are usually mounted at a height of 1.5–2 from the ground. If the site is not extreme in any way the results may hold good as representative for *square miles* (100 km^2). This is the *macroclimate.*

On the other hand if one wants the extremes in a region, in order to compare them climatically with the help of meteorological measurements, one is in the domain of *lococlimate** ("ecoclimate," Uvarov, 1931, p. 128; mesoclimate, Geiger, 1942, p. 3). Suitable examples are provided by slopes with different exposure to the sun, especially in the fjeld regions (examples: Ham-
450 berg, 1908, pp. 8–9; Frödin, 1915; Krogerus, 1937). The figures obtained may be considered representative for hundreds of square meters (100 m^2).

Finally, the *microclimate* operates within a much smaller unit area. These are the climatic conditions of *square meters* (m^2) and their fractions. Hence

*This expression was orally suggested to me by Lohmander.

microclimate can never be studied with the meteorological instruments set up in the usual way. The measurements have to be taken just above the ground and in the soil itself.

Temperature

Every attempt to correlate thermal conditions with animal or plant areas (for instance, isotherms and area limits) must at present be based on *macroclimatic* observations. To date sufficient measurements are available only in this field and—what is more important—lococlimatic and microclimatic conditions cannot be cartographically depicted for large geographical regions, such as Fennoscandia. It is always useful to keep this difficulty in mind. For the thermic microclimate at the most represents a reflection of the actual conditions over and in the soil, which is not only highly generalized but is even distorted (for example, Geiger, 1942, Fig. 34, p. 75).

Easily the commonest procedure is the correlation of the area limit—in our case primarily the northern limit—of an animal or plant species with an isotherm of the mean temperature for *one month*. Examples in the literature are so abundant that it seems superfluous to cite any. At any rate, in our climate, which is marked by very pronounced seasons, the use of isotherms for *the whole year* or even for one season (3 months or more) is to be avoided.

But even the isotherms for a single month have a highly variable "biological importance." For instance, the correspondence found by Heydemann (1931) between the January isotherms and the northeastern limit of *Selidosema plumaria* Schiff. (*ericetaria* Vill.), and that between the southern limit of *Colias palaeno* L. and the January isotherm of $-1°$ or $-2°C$ (Hesse, 1924, p. 387; Friederichs, 1930, p. 146), can only be coincidental and hence inconsequential, as shown by Warnecke (1931). For as soon as there is a snow cover, with its strong thermal isolation effect (Geiger, 1942, p. 159), the temperature of
451 the air in winter, as such, has virtually no effect on soil organisms (the geometrid mentioned above hibernates as a half-grown caterpillar). On the other hand it is quite possible that the January temperature is a definite expression of the area-limiting factor for *trees* sensitive to cold, such as *Ilex* (Holmboe, 1913).

In spring and autumn the daily variations are so large, with the temperatures often plunging below $\pm$ 0°C, that data on the mean temperatures also have little "biological importance." This situation is different in summer, when only in exceptional cases can the daily minima, and the maxima in our climate, do any direct harm to a very few stenothermic cold-loving organisms. The quantum of the "heat-sum" may be decisive at this time of year (see below for details), and this is fairly well expressed by the average monthly temperature. In choosing which of the three summer months to use, June is excluded because it shows large temperature anomalies in different

years (Ångström, 1938, Plate IV) and a considerable daily temperature range (Hamberg, 1914, Plate VI) with frequent night frosts (l.c., p. 39). Compared to July, August has the advantage of a smaller daily range, but normally has somewhat more marked minima (Hamberg, 1934, Plate XXVIII), in the north even fairly regular night frosts. Moreover, July is the warmest month of the year throughout Fennoscandia, whether the calculation is based on mean temperature, maxima, minima, or constant figures, and is hence in a way an exponent of the entire summer climate (Wahlgren, 1913, p. 162).

A. Summer Temperature

For the above reasons *July* must be considered the month whose average temperatures correspond closest to the biologically effective thermal component of the climate. I have therefore worked out an isotherm map based on the mean July temperature for Fennoscandia (Fig. 63). The data for Sweden are a simplification of those provided by Ångström (1946, Plate III), for Norway they are taken from the *Norske Meteorological Institute's Yearbook*, and for Finland from *Månadsöversikt* (1946) and correspondence with J. Keränen. However, I must note that the interpolation method used by Ångström (l.c.),
453 which gives an extraordinary degree of detail on the map, does not seem to be reliable. As I understand it, the isotherms in regions with scattered stations simply follow the altitude contours, which are subject to speculation especially in the cutoff ("Kupiert") parts of Norrland. It is characteristic that on the lower courses of the Pite and Ångerman rivers, and on the depression lakes in Hälsingland small "warm regions" with > 16°C can be indicated just because meteorological stations are located in or near these regions. Why should not similar high July temperatures occur in the other river valleys of Norrland, such as the regions of Över–Kalix, Harads, and Hällnäs, and on the rivers Kalix, Lule and Ume? The numerous botanically indicated "southern mountains," chiefly in Lappland, should also be shown on such a detailed map, but they cannot be depicted by any "interpolation method." A broader generalization of the isotherms, especially in north Sweden, would have made a more reliable impression.

If the new July isotherm map is compared with that by Ekman (1922, p. 311), significant differences are evident. Specifically, the center of heat along the big central Swedish lakes is much more pronounced. Likewise, southeast Norway is evidently more favored, and the "cold gaps" between the 15°C isotherms in central Norrland and in Osterbotten on the Finnish side have either disappeared or shrunk to a narrow strip in northern Ångermanland. The alterations may be partly due to actual climatic improvement (see p. 643), although this is less obvious in July than in the winter and spring months. But they are partly due to the denser network of stations.

We now come to the difficult task of selecting the species of carabids whose areas—on the basis of their distribution and ecology —may be influ-

452 Fig. 63. Mean temperature for July, 1.5–2 m above ground level, 1901–1930. After Norsk Meteor. Årbok; Ångström (1946); *Månadsöversikt av väderleken i Finl.* (1946); and Rubinstein (1927). Black = > 17° C; hatched = > 16° C; broken line = 15° isotherm. The standard 13° and 10° C isotherms are indicated only in Norway and in the high North, respectively.

enced by the July temperature (summer temperature). For this it will be best to take definite, thermally characteristic regions of Fennoscandia.

a. Plus-Districts

1. *Southeastern Norway*, especially the regions around the Oslo fjord. This is the only part of Norway where the July temperature reaches 17°C. A more or less isolated northward advanced occurrence in this region is shown by the following species:

454 *Abax ater*	*Cicindela hybrida*
*Amara montivaga**	*Lebia cyanocephala*
Carabus convexus	*Licinus depressus.*

2. *The interior valleys of east-central Norway,* chiefly the Gudbrands valley. In these valleys the 15°C isotherm swings conspicuously to north. The northernmost occurrence in Norway is particularly shown by the following species:

Amara fulva	*Cymindis angularis*
Anisodactylus binotatus	*Dyschirius politus*
Badister bipustulatus	*Harpalus puncticollis*
Bembidion gilvipes	*H. smaragdinus.*
B. properans	

3. *The innermost part of Sognefjord.* This is the most isolated and the mildest region in the whole of Fennoscandia. Correspondingly no fewer than 8 species occur here in complete isolation:

Agonum sexpunctatum	*Harpalus rubripes*
Amara curta (also near geiranger)	*H. tardus*
Anisodactylus binotatus	*Lebia crux-minor*
Carabus cancellatus	*Metabletus truncatellus.*

These three Norwegian "warm regions" are of course also characterized by other climatic features, primarily by relatively low precipitation and more hours of sunshine, as described below (p. 497) in detail. Yet we might be fully justified in considering the summer heat—here represented by the mean July temperature—as the most important factor for the above-mentioned species. This will be evident from the comparison below with species that are *favored* by the oceanic west Norwegian climate.

Especially interesting among the above 8 "Sogn species" are *Carabus cancellatus*** and *Metabletus truncatellus,* both of which are flightless. Under the

*However, the present distribution of *Amara montivaga* is strongly influenced by the history of immigration (p. 631).

**If the record of a solitary specimen of *Carabus cancellatus* in Sogn is to be attributed to transport by man, the same cannot be said of *Metabletus truncatellus,* which is widely distributed in the above-mentioned region. *Metabletus* is dimorphic, but the macropterous form is extremely rare; 7 specimens studied from the inner Sogn were all brachypterous.

455 present climatic conditions they could hardly have immigrated to the Sogn region, which is completely cut off to the north, east and south by the *Regio alpina* of the fjelds (see also p. 688).

In the small "17°C regions" along the Swedish west coast no especially heat-loving carabids have been discovered. At present it is not possible to decide whether the isolated records of *Calosoma reticulatum* and *Pogonus luridipennis,* the first was possibly more or less accidental, were made at places where meteorologically a favorable "lococlimate" has still not been established. It would be better to consider *Anthicus gracilis* Panz (Jansson, 1927, p. 222), which in addition to the warm region of North Bohuslän also occurs in southeast Norway. The matter is still clearer in the case of *Sphingonotus coerulans cyanopterus* Charp., which is common in the region of Strömstad and was also found along the Swedish west coast only in the "warm region" near Göteborg (Hånsson, 1902, p. 33); also in southeast Norway (see also Kvifte, 1941, p. 42) but not in Denmark. The species has therefore been considered a "xerothermic relict" (Wahlgren, 1917, p. 100; Ander, 1942, pp. 16 ff.). Ander (1942, 1947) also applies this explanation to the occurrence of *Scolia hirta* Schrk. near Särö in northern Halland and in southeastern Norway. The July isotherm map renders this assumption plausible. On the border between Sweden and Norway close to the coast insolation conditions are, in addition, extremely favorable (p. 497).

4. *The central Swedish lake district*, especially around lakes Mälaren and Hjälmaren. The character of this part of Sweden as the biggest summertime warm region of the whole of Scandinavia is becoming evident with the new July isotherm map (Fig. 63) (cf. the older map by Ekman, 1922, p. 311). The fauna of this region is actually extremely rich and includes a strong markedly southern element, which I have already considered (Lindroth, 1943a, p. 139) very briefly in connection with Coleoptera. Among the carabids, in the first place, the following are the "central Swedish heat-requiring[†] species" (x = xerophilous):

Agonum dorsale x	*Harpalus anxius* x
A. lugens	*Licinus depressus* x
Badister sodalis	*Odacantha melanura*
B. unipustulatus	*Oodes gracilis*
Brachynus crepitans x	*Panagaeus bipustulatus* x
Demetrias imperialis	

456 Secondly mention may be made of: *Harpalus rufitarsis* and *Microlestes minutulus*, which have been found only in the Vättern region, and *Demetrias monostigma*, *Leistus ruformarginatus* and *Microlestes maurus*, found only in the Vänern region.

†(cf. p. 305 ff.; suppl. scient. edit.).

On the other hand the more or less isolated occurrence, in the same regions, of species like *Amara montivaga, Bembidion transparens* and *Dichirotrichus rufithorax* is chiefly due to their history of immigration. All of them are demonstrably late immigrants to Sweden (see p. 630).

Ecologically the 11 species listed above can be readily divided into two groups: *xerophiles,* marked with an "x" and *hygrophiles,* i.e. the remaining 6 species.

I paid special attention to this latter group in the contribution cited above (1943a). Apart from other Coleoptera it includes numerous representatives of carabids. Zoogeographically it is easy to arrange them in a continuous series and also to classify them into four main types:

a) There is a more or less uninterrupted connection of the central Swedish area along the east coast (where the July map shows some high values) toward the south. These are evidently less typical heat-requiring species and are not considered above. Examples are: *Agonum livens*, *Badister dilatatus*, *Oodes helopiodes*, *Pterostichus gracilis*.

b) The direct connection of the area is interrupted southward, but the species concerned are found again on Öland and Gotland and in the southernmost mainland provinces of Sweden: *Agonum lugens*, *Badister sodalis*, *B. unipustulatus*, and *Odacantha melanura*.

c) The species are also missing from Öland and Gotland, so that the gap in distribution becomes very wide. Examples of these are found only outside the family Carabidae: *Oedemera croceicollis* Gyll., *Psammobius bipunctatus* Fbr., *Reichenbachia impressa* Panz., *Silis ruficollis* Fbr.

d) The species are completely missing from Scandinavia outside the central Swedish lake district: *Demetrias imperialis* (for a possibly accidental occurrence on Fårön, see p. 287), *Oodes gracilis*; *Euconnus rutilipennis* Müll., *Stenus solutus* Er. (the record from Skåne in the *Catalogue*, 1939, remains unconfirmed).

Here we need not venture an opinion as to whether a relict phenomenon is involved here (cf. p. 687). However, these distribution types at any rate
457 show that the central Swedish lake district *must* be climatically favored in some way. The following account of other climatic factors will show that such a pronounced advantage derives only from summer temperature conditions. The view expressed earlier (Lindroth, 1943a, p. 139) might therefore be justified, namely that "the locally (microclimatic) elevated midsummer temperature of shallow, eutrophic lakes accounts for the favorable nature of the central Swedish lake district."

However, even the 5 xerophiles ("x") of the above list show a similar occurrence in central Sweden, which is more or less isolated (especially in the case of *Harpalus anxius,* least in the case of *Panagaeus bipustulatus*). We are
458 therefore justified in assuming that the favorable thermal conditions in central Sweden affect chiefly, but not exclusively, the limnetic biotopes, i.e. it is

457 Diagram 48. Temperature preferenda of three central Swedish "heat-requiring" species, each compared with a more widely distributed relative.

a—*Agonum lugens* (1) and *A. viduum* (2); Experiments 2–3 (p. 70); b—*Badister unipustulatus* (1) and *B. dilatatus* (2); Experiments 4–5 (p. 70); c—*Oodes gracilis* (1) and *O. helopioides* (2). *Oodes* species according to Lindroth, 1943a.

a *macroclimatic* situation affecting the entire living world, and this concept is therefore fully confirmed by the new July map by Ångström (1946).

It is naturally important to verify experimentally whether the assumed "heat-requiring species" of central Sweden are actually thermophilous. A few such experiments were performed, chiefly in the temperature gradient apparatus, where the "comparison species" were always simultaneously studied. Diagram 48 shows the behavior of three pairs of strongly hygrophilous, ecologically closely-related species in the temperature gradient apparatus. In each pair—geographically speaking—the "heat-requiring species" shows a preference 2.8–5.6°C higher than that of the more widely distributed comparison species.* The lower response point was studied only in the species of *Oodes* and *Demetrias imperialis* (Lindroth, 1943a, pp. 137, 143). Both the adult and the larva of *gracilis* showed considerably higher values than the adult of *helopiodes*. But in *Demetrias* these figures were much lower. The preferenda in this case might reflect a zoogeographically more important characteristic than the response point.

Of the *xerophiles*, *Harpalus anxius* and *H. rufitarsis* were† tested from among the presumed "limestone species" (pp. 130 ff.). In the latter species the temperature preferendum is extremely high, in *anxius* it is lower but still higher than in *hirtipes* (and in the widely distributed species *aeneus*, *tardus* and *seladon*). Also with regard to the lower response point to temperature, *rufitarsis* shows far higher values than *anxius*, in which, strangely, it is extremely low. *Brachynus* and *Agonum dorsale*, which have been thoroughly compared (pp. 59 ff.), have low preferenda (in comparison with the species of *Harpalus*) but a much higher low response point (even higher than in *Harpalus azureus*).

The experiments thus give the clear impression that the central Swedish "heat-requiring species" do actually have a thermal requirement. As a rule this is evident from the high temperature preferendum. Hence the temperatures
459 in *summer* seem to be most significant, and our idea that the July isotherms provide a true picture of the central Swedish warm region of the fauna is strengthened.

5. *The inner parts of south Finland.* The July isotherms here, especially those of 16° and 17°C, swing strikingly northward. Let us find out whether this can explain the well-known fact that many animals in Finland have their northern limit much beyond that in Scandinavia.

Among the carabids the following more or less pronounced cases may be mentioned:

*The low values for the species of *Badister* are probably to be explained by their pronounced hygrophily (see p. 68).

†(Cf. p. 215 ff.; suppl. scient. edit.).

Acupalpus dorsalis
A. flavicollis
Agonum livens
A. obscurum
Amara aenea
A. equestris
A. montivaga
A. similata
Anisodactylus binotatus
Asaphidion flavipes
Badister bipustulatus s. l.
B. dilatatus
B. peltatus
B. sodalis
Bembidion andreae polonicum
B. articulatum
B. biguttatum
B. humerale
B. nigricorne
B. ruficolle
B. unicolor
B. varium
Broscus cephalotes
Carabus cancellatus
C. granulatus
Cicindela hybrida
Dromius marginellus
Dyschirius lüdersi
Harpalus anxius
H. smaragdinus
H. tardus
Lebia chlorocephala
Microlestes maurus
M. minutulus
Nebria livida
Oodes helopioides
Pterostichus angustatus
P. cupreus
P. gracilis.

In the case of some of these species, for example, *Bembidion nigricorne*, *B. ruficolle*, *Dyschirius lüdersi*, it is natural to look for the basis of their wider distribution in Finland in the history of immigration. This is especially clear in species (for example, *Panagaeus crux-major* and *Pterostichus vernalis*, as also *Amara nitida* and *Pterostichus niger*) that have already spread into the Swedish region (in Nbt). Even in an extreme case, such as that of *Bembidion biguttatum*, which is known in Scandinavia with certainty only from Skåne, one would not suppose that the species has actually reached its existence limit
460 there. Otherwise one would be misled into believing that the East Baltic stock is physiologically different, with a lesser heat requirement. These questions are discussed elsewhere (p. 732).

But it is out of the question that the marked incidence of a more northerly northern area limit in Finland is determined by existence ecology. Ekman (1922, pp. 357 ff.) alluded to this problem. He gives a list of no fewer than 23 mammals and birds that have spread east of the Baltic Sea much farther north than in Scandinavia. He implies that factors relating to the immigration history have had the main role, but does not examine the important question whether the climatically favorable conditions in Finland may not have contributed to the slanting Fennoscandian northern limit. It is not improbable that, for instance, the northern limit of the thrush-nightingale (*Aëdon luscinia*)* is dependent on the thermal conditions in early summer. In recent

*Now known as *Luscinia luscinia*—General Editor.

decades, characterized by increased temperatures (see pp. 643 ff.) it has considerably expanded its Swedish area northward. The northern limit of the *polecat* (*Putorius putorius**, according to Kalela (1940a), is dependent on thermal conditions as well, at least in Finland.

That the high northern limit of some carabids in Finland must actually be thermally determined, so that many species have reached their existence limits *on both sides* of the Baltic Sea, is evident from the fact that even some of the species whose more or less isolated occurrence in the central Swedish lake district characterizes them as pronouncedly "heat-requiring," belong to the group with the "slanting northern limit." Of the 16 species mentioned above (p. 455) one-half attain a more northerly position in Finland**:

Badister sodalis	*Microlestes maurus*
B. unipustulatus	*M. minutulus*
Demetrias monostigma	*Odacantha melanura*
Harpalus anxius	*Panagaeus bipustulatus.*

The heat requirements of 2 of these species were experimentally studied (see above).

One may also adopt the consideration of Ekman (1922, p. 368), that the pronounced east Scandinavian species ceases to occur in coastal southern Norway: If this limit were determined by *dispersal* factors "it would be rather
461 strange that all the species should have remained static just at the western boundary of the country" (original in Swedish). In the present case it is striking that among the carabids considered here, several species have almost the same northern limit, which forms a slanting line through central Finland at about the latitude of Kuopio. Clear exponents of this type are: *Agonum obscurum*, *Amara aenea*, *A. montivaga*, *Asaphidion flavipes*, *Badister bipustulatus* s. l., *Broscus*, *Harpalus smaragdinus*. This conjunction of the northern limit of a larger number of species would be incomprehensible if it were assumed that it was determined by dynamics (dispersal ecology, history of immigration). Yet the July isotherms correspond completely. It is noteworthy that the same 7 species—with the exception of *Amara montivaga*, which is in process of dispersal west of the Baltic Sea (p. 632)—show a largely common northern limit in Scandinavia too. A more southerly group in Finland, with the northern limit in the east around latitude 62° N, comprises *Badister dilatatus*, *Bembidion articulatum*, *Microlestes minutulus*, *Pterostichus angustatus,* etc. In Scandinavia the northern limit of these species also runs much farther south than that of the earlier group.

The assumption is therefore fully permissible, *that animals that have advanced considerably farther north in Finland than in Scandinavia have in some*

*Now known as *Mustela putorius*—General Editor.

***Agonum dorsale* and *Brachynus* are excluded because their occurrence in Finland appears to be more or less accidental.

cases actually found their existence limit on both sides of the Baltic Sea. It is difficult to detect the deciding factors outside the *climate*. Moreover, among the climatic factors I am not aware of any in the interior of Finland that might prove as favorable a condition as *the summer temperature*, as expressed in the lay of the July isotherms. These mean temperatures evidently do not represent the decisive factor—it would be more correct to work with the *heat-sums* of the summer (also see p. 479). But they give a general idea of the temperature conditions, which cannot be far wrong *for the summer* (cf. p. 451). Moreover, the inner parts of Finland compares favorably with Scandinavia with regard to the frequency of the temperature maxima in summer (Enquist, 1929, p. 20, Fig. 8).

6. *The surroundings of the northern end of the Gulf of Bothnia.* In Ek-
462 man's July isotherm map (1922, p. 311) the 15°C isotherm shows an isolated warm region here. In the new map (Fig. 63), based on the figures of the period 1901–1930, this isolation—at least partly on account of climatic improvement—is accentuated toward the east, and in Sweden in the plains there is an insignificant gap with $<$ 15°C only in northern Ångermanland. Now if the isotherm of 15.5°C were drawn—the necessary meteorological observations are not available with me—the characteristic of this region as a heat center in midsummer, even though poorly marked, would be evident. Species like *Agonum versutum*, *Amara tibialis*, *Pterostichus vernalis* and *Synuchus nivalis* here have their northernmost occurrence, not only in Fennoscandia but throughout their total area. Especially interesting are three species that were found more or less isolated in the same regions, north of their total area. These are:

Chlaenius nigricornis   *Panagaeus crux-major.*
Dromius longiceps

It is highly likely that in these cases too the favorable summer temperature has been decisive. Elsewhere (p. 674) reasons are given for considering the occurrence of *Agonum thoreyi* in these regions as a relict from the postglacial warm period.

b. Minus-Districts

1. *The thermally unfavorable western and northern coast of Norway.* With the exception of the inner parts of the most incisive fjords (Hardanger fjord and Sogne fjord) the entire Norwegian coast from the southern tip of the country lies outside the 15°C July isotherm. Examples of species that avoid these summer-cool coastal regions were provided in the context of the "plus-districts" along the Sogne fjord and the northerly position of many northern limits in Finland.

It is easy to draw up a considerably longer list of species that have not crossed at all or have crossed only at isolated points of the main Scandinavian watershed to the west. The latter are in parentheses.

(*Agonum ericeti*)
(*A. piceum*)
(*A. quadripunctatum*)
(*A. sexpunctatum*)
A. versutum
(*A. viduum*)
463 *Amara famelica*
A. fulva
A. littorea
A. municipalis
(*A. ovata*)
(*A. tibialis*)
(*Bembidion doris*)
B. gilvipes
B. guttula
(*B. lampros,* only in the north)
(*B. obliquum*)
(*B. quadrimaculatum*)

(*Carabus clathratus,* in the north)
Chlaenius nigricornis
Cicindela silvatica
Dromius sigma
Dyschirius politus
(*D. thoracicus*)
(*Harpalus aeneus,* in the north)
Lebia crux-minor
Metabletus truncatellus
(*Notiophilus palustris,* in the north)
(*Pterostichus coerulescens,* in the north)
(*P. lepidus,* in the north)
(*P. minor*)
(*P. vulgaris,* in the north)
(*Synuchus nivalis,* in the north)
(*Tachyta nana*)
Trechus quadristriatus.

This group is in no way homogeneous. Several of these species—especially those that never reach the actual fjeld areas—could be prevented from entering western Norway "mechanically" by the chain of fjelds (cf. p. 614). Then again, where there may be reason to assume that the animal cannot live on the west Norwegian coast due to special existence requirements, it is not certain at all that the summer temperatures—or the thermal conditions in general—are decisive. The Norwegian coast has other peculiarities, with respect to precipitation and insolation and, moreover, there is the condition of the soil (p. 512). Let us therefore postpone a discussion until we can make a comparison with species that are apparently *favored* by the west Norwegian climate (p. 474).

2. *The upland of South Sweden* (in the provinces of Småland and Västergötland). As an isolated "minus-district" this is especially interesting. The mean July temperature of the central part does not reach 15°C, a figure that comes down again only in northern Värmland.

The fauna of the south Swedish upland is poor. The phenomenon that species of the southern distribution type completely or partially avoid these regions—as proven by the maps in Part II of this book—is so extraordinarily frequent that any enumeration of examples would be superfluous.

464 However, it is not to be assumed that exclusively climatic factors operate in this connection. The condition of the soil, especially the almost complete absence of loam, plays a decisive role for certain species; conversely species that require fine sand and the like, for example *Asaphidion pallipes*, *Bembidion litorale*, are favored in these regions. The dearth of limnetic molluscs in these regions seems to be chiefly due to chemical factors (Hubendick, 1947).

Climatically the south Swedish upland is unfavorably disposed in almost every respect. In every season the temperature is lower than in the adjoining coastal areas (see also p. 474), the precipitation, especially in the west, is abnormally high (Fig. 73) and the insolation consequently low (Fig. 76). It seems scarcely possible to decide in individual cases which climatic factor has been responsible for preventing the entry of a species into the south Swedish upland. In some cases the distribution gap may have arisen under the combined effect of several of these factors.

For the climatically dependent northern species a cool region evidently signifies a "plus-district." In fact it is strange that the south Swedish upland does not show more northern forms, whether "relicts" or not. The only clear case is that of *Pterostichus adstrictus*, which is a counterpart of *Saussurea alpina* among the plants (Erlandsson, 1940). Moreover, in these regions *Miscodera* and *Patrobus assimilis* show greater frequency and abundance. These facts are undoubtedly climatically determined, but it remains undecided whether the low summer temperature, the short duration of the annual life cycle or some other factor has been effective.

3. *The fjeld regions and the Far North.* It is obvious that the more or less specifically fjeld and tundra animals, which in Fennoscandia have a distinct southern limit, *tolerate* low temperatures both in summer and in winter. However, it is not as certain that they also *require* low temperatures, and hence respond negatively to moderate heat and are thereby adversely affected. Brundin (1934, pp. 159–160), in connection with the most pronounced high alpine species of the Fennoscandian carabid fauna, *Nebria nivalis*, actually surmised that its almost complete restriction to the *Regio alpina* is understandable chiefly by the "low competition limit" of the species. Earlier (1935a, p. 616) I took issue with this.

465 The question can be resolved only experimentally. I have not carried out any such experiments, but Krogerus has permitted me to publish here the temperature gradient apparatus experiments with Nordic carabids that he carried out during our stay together at Abisko in July, 1939. The readings with the apparatus were taken according to temperature classes, so the results are given differently than those of the other temperature gradient apparatus data. Other experiments with the same species are given separately (Table 31). The humidity of the air was regulated with wet cotton at the warm end of the apparatus.

Krogerus' experiments show that *Nebria nivalis* by far surpasses all other species in respect of marked "thermophoby." Even at mild temperatures this species showed an alarm response, whereas at the cold end of the apparatus both cleaning response and copulation were observed.

It is interesting that among the species investigated *Agonum consimile*, despite its restricted distribution to the fjelds and to the Far North, has the highest preferendum. However, in contrast with the other species, this carabid
466 lives on wet bog soil (not *Sphagnum*!), at sites exposed to sun, where the soil

465 **Table 31. Temperature gradient apparatus experiments with Carabidae of the Far North (Krogerus)**

Dash (–) means this temperature was not represented in the experiment

	Temperature, number of individuals									
	5°	8°	10°	12°	15°	20°	25°	32°	35°	Mean
Agonum consimile	0	5	4	1	9	6	0	0	–	13.9°
Bembidion hasti	1	5	4	1	2	2	0	0	0	11.1°
B. hyperboraeorum	–	–	22	1	2	0	0	0	–	<10.0°
” ”	5	0	8	4	3	0	0	0	–	9.9°
” ”	5	10	7	1	2	0	0	0	0	8.7°
Dyschirius helléni	0	0	5	2	3	0	0	0	–	11.9°
” ”	0	4	5	1	0	0	0	0	0	9.4°
Nebria gyllenhali f. typ.	4	0	3	0	1	0	0	0	–	8.1°
” ” ” ”	10	6	4	4	1	0	0	0	0	8.0°
” ” *f. ruf.*	8	0	2	0	0	0	0	0	–	6.0°
” ” ” ”	8	1	1	2	0	0	0	0	0	6.8°
N. nivalis	–	–	7	0	0	0	0	0	–	<10.0°
” ”	5	0	0	0	0	0	0	0	–	< 5.0°
” ”	5	0	0	0	0	0	0	0	–	< 5.0°

is well-warmed in summer. It is pronouncedly heliophilous.

On the other hand *Nebria gyllenhali*, which advances south as far as to Lake Vättern and Gotland, always seeks out cold shorelines in low or southerly places. Around the Gulf of Finland, where it is permanently native only on the southern shore, this might be (as on Gotland) due to seepage of cold groundwater at the limestone cliffs of the Estonian coast. Whether the fact that in the experiments the *forma rufino* showed a greater cold requirement means it is physiologically (genetically?) different from the *forma typica* must remain undecided. I am not inclined to think so.

But we may be justified in seeing in these experiments* confirmation of the idea that animals with Nordic and/or alpine distribution have a positive response to cold and a real requirement for cold, and that for them these characteristics represent the most important area-limiting factors. Probably no one seriously doubted this.

On the other hand it might be correct to consider the southern limit of Nordic plants as largely a *competition limit*. However, their southernmost outposts often have a pronounced "Nordic" microclimate or lococlimate (for example, Helms and Jørgensen, 1924, p. 296).

In Fennoscandia this area-limiting "thermophoby" of markedly alpine species may produce a bicentric area. The temperature maps for every season show that the cold zone along the Scandinavian chain of fjelds is distinctly

*See also the temperature gradient apparatus experiments by Krogerus (1937, p. 299; 1939, p. 1223) with *Bembidion difficile*, *Dyschirius helléni* and *Elaphrus lapponicus*.

interrupted in the Province of Jämtland, which may cause a purely existence-ecological gap (repeatedly, as established by other authors) for animals and plants with a high cold requirement. Whether, as seems likely, the *summer* temperature (expressed fairly by the July isotherms) is decisive remains to be established. However, we cannot rule out a *thermally* determined bicentricity even where one would be inclined to ascribe this phenomenon to the immigration history (cf. p. 752).

467 B. The Temperature in Spring and Autumn

It has been emphasized by several biogeographers that the common attempt to "explain" the area limits of animals and plants by the *mean* day temperatures (of the year, of a season, of a month, etc.) is inadequate, because daily averages represent biologically effective factors absolutely incompletely (Samuelsson, 1915; Ekman, 1922, pp. 309 ff.; Enquist, 1924, pp. 204 ff.; Hård, 1924, pp. 12 ff.). However, we discussed the use of mean summer temperatures for this purpose earlier (p. 451) chiefly from July.

It is not enough to have an idea of the extent of midsummer heat: we must also study the duration of the yearly life cycle. This is determined by the thermal conditions of the "critical months" (Lindroth, 1931, p. 480). In Fennoscandia these months are April or May in spring (probably even June in the fjelds), and September or October in autumn. However, it would be erroneous to work out the daily mean temperatures for these seasons; in this context the *minima* are decisive.

I have therefore drawn the *isotherm maps of the average minimum temperatures* for the above-mentioned four months for the period 1920–1939 (Figs. 64–67). Since it is undoubtedly easier to study the factors that affect the length of the yearly life cycle from one map, and since, as far as I can see, a late spring can be biologically compensated by a late autumn (and vice-versa), I have prepared on the basis of the same figures an April + October map (Fig. 68) and a May + September map (Fig. 69). The first might be applicable to the more southerly parts, and the second to more northerly parts of Fennoscandia. At any rate the lay of the April + October isotherms may be biologically inconsequential where it gets colder than ± 0°C.

For comparison I give the April + October and May + September maps of the *average day temperature* (Figs. 70, 71). These are of course based on the figures for a longer and, in part, earlier period. But it was intended only to compare the maps of the averages and of the minima, so this may not matter. Detailed comparison is impossible because of the unequal distribution of stations and the broad generalization of isotherms in the minima maps.

473 The remarkable correspondence confirms Langlet's view (1935, pp. 311 ff.) on the close correlation between mean and extreme temperatures. The minima

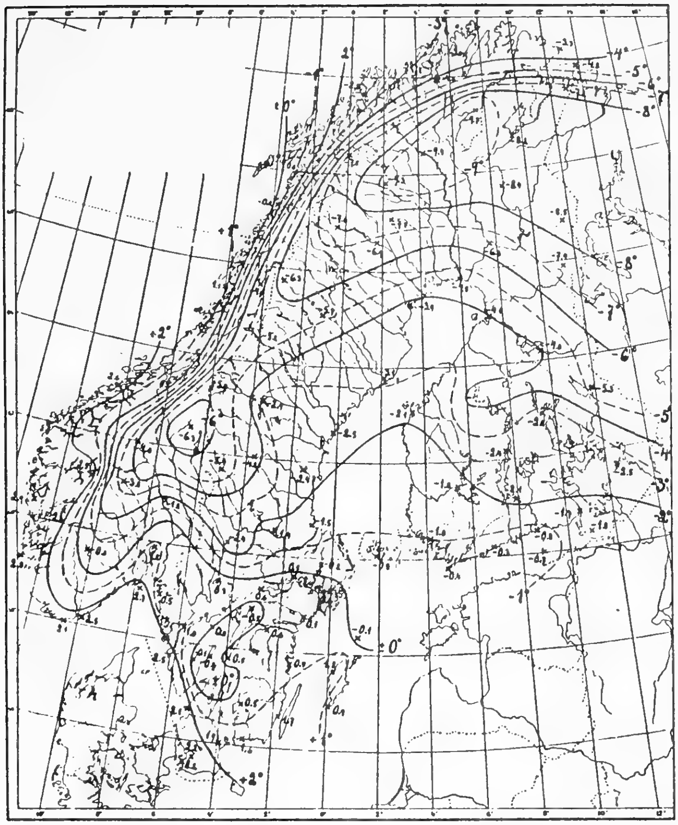


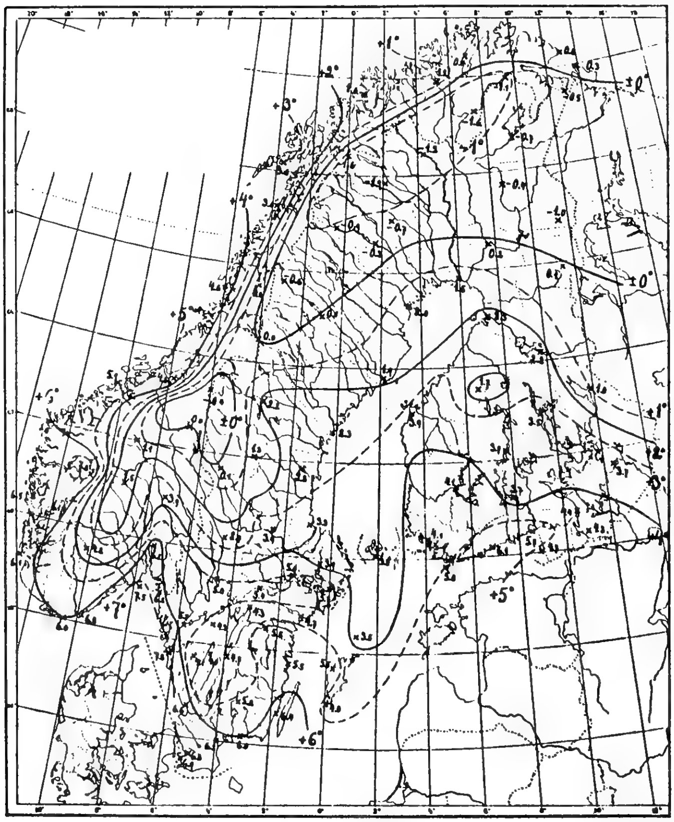
Fig. 64. April. Mean minimum temperature (1920–1939). Sources: cf. Fig. 68.

of course primarily favor more the Norwegian west coast Öland-Gotland but also the Finnish coast on the Gulf of Bothnia not only in comparison with the inland but also in comparison with the Swedish coast across the Baltic. The latter may be due primarily to the course of the currents in the Bothnian Sea (see map in Fig. 19, p. 247). Comparable with regard to the contents are the maps published by Hamberg (1914, p. 40) on the mean number of days with frost (days with minimum temperature < ± 0°), although they are limited to Sweden (Fig. 72). Here it becomes more evident that the south Swedish upland is not favored. The intense exposure of localities to frost there is noted by Hård (1924, p. 15). Concerning the biological (and biogeographical) effect of autumn frost, see also Eklund (1937, pp. 323 ff.).

In no part of the annual period of activity is *the Scandinavian west coast* thermally more favored than in autumn (September, October). But in spring this is almost alike because of the Gulf Stream, the cooling effect of seawater at this time is eliminated on the Baltic coast. Obviously species that extend far north up the Norwegian coast are thermally very susceptible in the "critical" months.

The best example of species that reach *higher latitudes in Norway than in the rest of Fennoscandia,* even the highest of their total area are:

Agonum assimile	*A. lunicollis*
A. ruficorne	*Bembidion femoratum*
Amara bifrons	*B. lunatum*
A. ingenua	*B. nitidulum*



468 Fig. 65. May. Mean minimum temperature (1920–1939). Sources: cf. Fig. 68.

469 Fig. 66. September. Mean minimum temperature (1920–1939). Sources: cf. Fig. 68.

Bradycellus collaris	*Olisthopus rotundatus*
Calathus fuscipes	*Patrobus atrorufus*
Carabus coriaceus	*Pterostichus niger*
C. hortensis	*P. strenuus*
Cicindela campestris	(*Trechus discus*)
(*Dromius quadrinotatus*)	(*T. micros*)
Leistus ferrugineus	*T. obtusus*
Nebria brevicollis	*T. secalis*
N. salina	*Trichocellus placidus.*

But the distribution type of these species is not climatically determined to the exclusion of all else. Reasons of immigration history have primarily determined the predominantly western (partly also northern) area of *Bembidion*

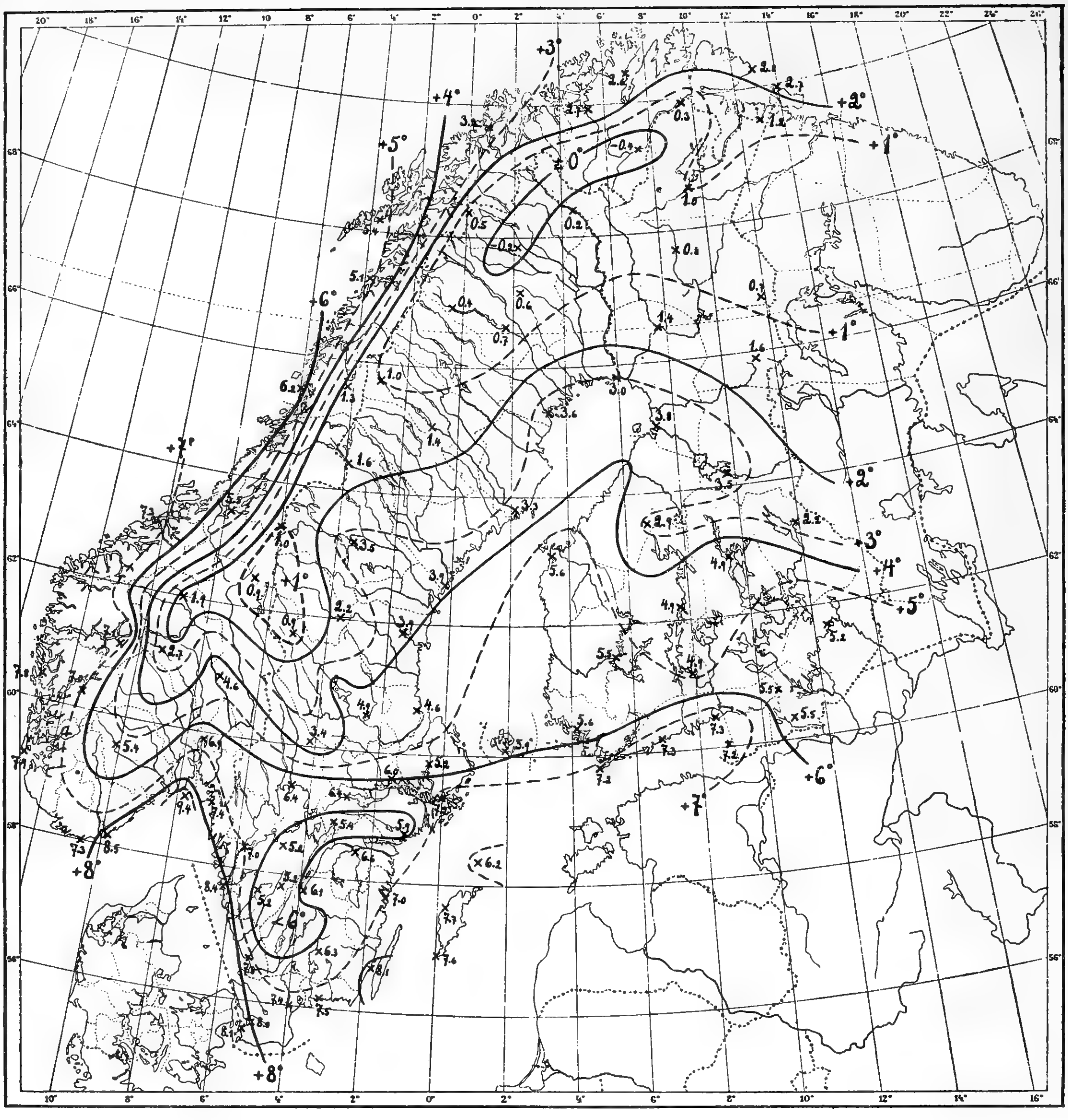
469 Fig. 67. October. Mean minimum temperature (1920–1939). Sources: cf. Fig. 68.

femoratum (p. 744), *B. nitidulum* (p. 745), *Trechus obtusus* (p. 762), and probably also of *Bradycellus collaris* (p. 397) and *Pterostichus strenuus* (p. 395). In *Dromius quadrinotatus* it is possible that its isolated, northernmost occurrence is due to passive dispersal (p. 320). Finally, both species of *Trechus* are missing from the western part of the country and both were found, totally isolated, only in two locales each in the Trondheim region.

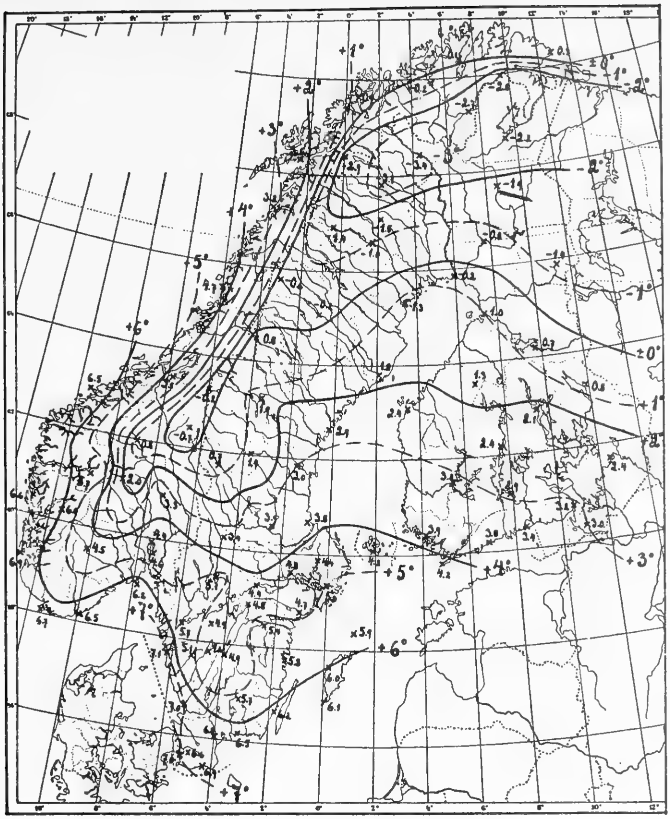
475 The remaining 18 species in the list to a large extent clearly have climatically determined areas. Eight of them (*Agonum assimile*, *Amara bifrons*, *A. ingenua*, *Carabus hortensis*, *Patrobus atrorufus*, *Pterostichus niger*, *Trechus secalis*, *Trichocellus placidus*) have a markedly slanting northern limit in Finland. This is in sharp contrast with the "July species" treated above (p. 459). Corresponding with the lay of the minimum isotherms of the "critical" months,

470 Fig. 68. April + October. Mean minimum temperature of air at ground level (1920–1939).

From *Norsk Meteor. Årbok*; *Meteor. Jahrb. f. Finnl.* (until 1937); J. Keränen (in litt.); and journals of *Sveriges Meteor.-Hydrol. Inst.*



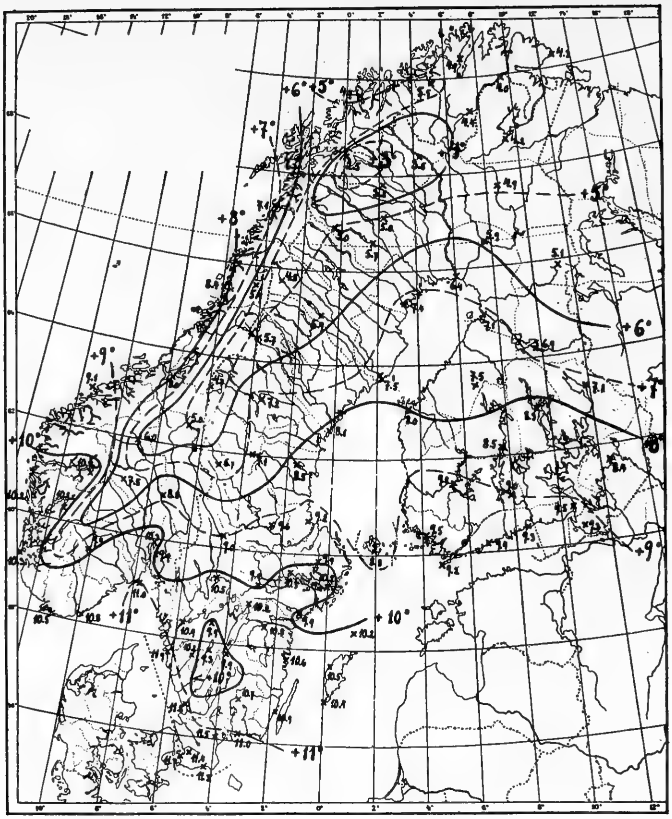
471 Fig. 69. May + September. Mean minimum temperature of air at ground level (1920–1939). Sources: cf. Fig. 68.



472 Fig. 70. April + October. Mean temperature of air at ground level (1901–1930) at same (neighboring) stations as in maps, Figs. 64–69. From Norsk Meteorol. Årbok; Sver. Meteor. Hydrol. Inst. Årsbok; Månadsöversikt av väderleken i Finland (1946); and J. Keränen (in litt.)

it runs *from southeast to northwest*, which means that toward the north these carabid species avoid a continental climate. The gap in the Oslo fjord region concerning the distribution of *Nebria salina* is also instructive, and to a lesser extent that of *N. brevicollis*. Any other interpretation than that of a climatically-determined existence limit seems to be erroneous in this case (both species are capable of flight). The Fennoscandian northern limit of *Nebria salina* even coincides with the +2.5°C isotherm of the minimum temperature of April + October (Fig. 68). In a similar way *Agonum assimile* can be compared with the corresponding +3.5°C isotherm, and *Calathus fuscipes* with the +4.5°C isotherm for May + September (Fig. 69).

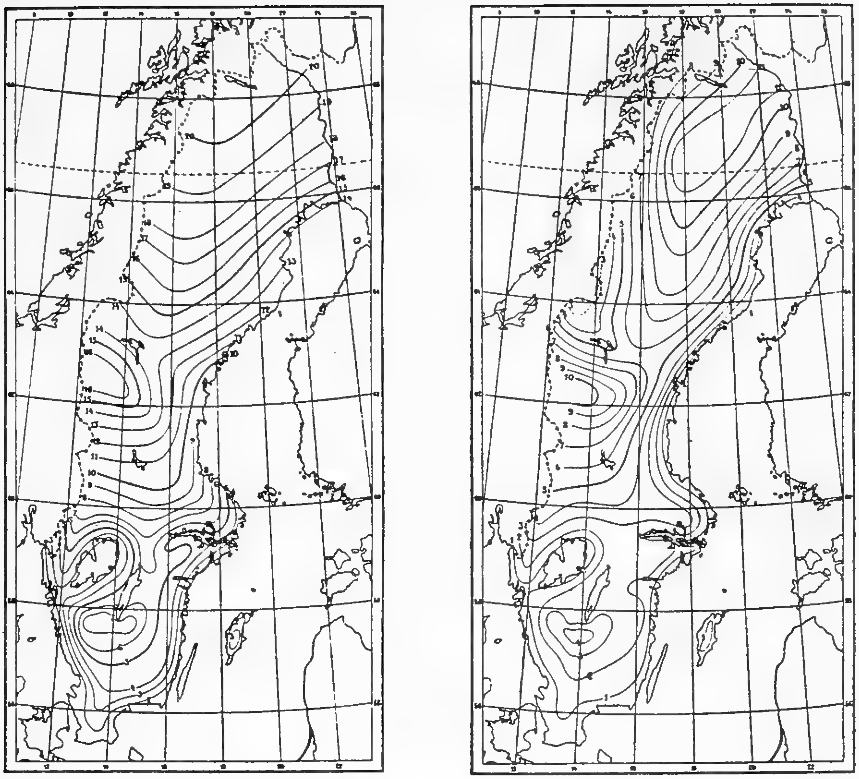
If the view expressed here is correct: that at least 18 species of the above



472 Fig. 71. May + September. Mean temperature of air at ground level (1901–1930). (Sources: cf. Fig. 70).

list are clearly favored by the oceanic west Norwegian climate—the question arises whether the ecology or some other aspect of the biology of these carabids does not provide an indication as to which of the climatic factors are the most important, and why these have influences just on these species and so effectively.

One is reminded of an observation made by S.G. Larsson (1939, pp. 510 ff.). He found that the number of *larval hibernators* ("autumn reproducers") among the carabids in Europe increases toward the west, especially toward the northwest; it is highest on the North Atlantic islands (see p. 329). He divided the Scandinavian carabid fauna, which according to him includes 25.2% autumn reproducers, into five geographical groups, and gives the following percentages of "autumn insects":



473 Fig. 72. Mean number of days with frost (1881–1911) in May (left) and September (right). After Hamberg, 1914 (p. 40).

1. South Scandinavian group: 23%
2. West Scandinavian group: 89% (possibly 100%)
3. East Scandinavian group: 7%
4. Pan-Scandinavian group: 41%
5. North Scandinavian group: 23%.

These figures are of course not very correct with regard to our present knowledge, for some new species have since been added to the Scandinavian
476 fauna, and there are others which cannot be placed in the distribution groups suggested by Larsson. Moreover, it has been shown that a larger number of species, at least in Scandinavia, belong to a different reproduction type than

Larsson assumes, which is pointed out in Part I against each of the species concerned. The Scandinavian carabid fauna as a whole may include 24.6% species that hibernate exclusively or regularly as larvae. The other figures deviate insignificantly from Larsson's*. At this point attention has only to be paid to the detailed consideration of the development types (p. 568). But the principle discovered by Larsson stands established: *In Scandinavia the number of larval hibernators increases tremendously toward the west.*

If this principle is applied to the species grouped above on the basis of the position of their northern limit we find the following:

1. Among the 39 species which in Finland advance farthest north (p. 459) there are 5 species (*Amara equestris*, *Broscus*, *Cicindela hybrida*, *Harpalus smaragdinus*, *Nebria livida*), i.e. 13%, that regularly hibernate as larvae.

2. Among the 35 species that advance far into Sweden but avoid the Norwegian west coast (at least in the north) (p. 462), 7 species, i.e. 20%, are more or less regular larval hibernators (*Amara fulva*, *A. municipalis*, *Cicindela silvatica*, *Pterostichus lepidus*, *P. vulgaris*, *Synuchus*, *Trechus quadristriatus*).

3. Among the 26 species whose area in Norway reaches the highest latitudes (p. 474), there are 15 more or less regular larval hibernators, i.e. 58%, (*Amara bifrons*, *Bembidion lunatum*, *Calathus fuscipes*, *Carabus coriaceus*, *C. hortensis*, *Cicindela campestris*, *Leistus ferrugineus*, *Nebria brevicollis*, *N. salina*, *Olisthopus*, *Patrobus atrorufus*, *Pterostichus niger*, *Trechus discus*, *T. obtusus*, *T. secalis*). If we subtract the 8 species either missing in the western part of the country or having a distribution due to historical reasons (p. 474) the number of larval hibernators increases to 72%.

It is scarcely possible to explain these conditions in any way other than as follows (expressed in other words by Larsson, 1939, pp. 526–527): *The most*
477 *important area-limiting climatic factors are those which affect the developmental stages.* Hence the chief climatic requirements *for adult hibernators are a warm summer, and for larval hibernators mild "critical" months* in spring and autumn. The temperature conditions in the dead of winter may have a very secondary role in both cases.

As we have seen, there is no lack of exceptions to this rule. But they are mostly understandable. The 12 "eastern" larval hibernators (enumerated above under Points 1 and 2)—with the exception of *Nebria livida* (see below) and *Pterostichus vulgaris*—are all more or less pronounced *xerophiles*. Among the 15 "western" larval hibernators there are only 2 (*Amara bifrons*, *Olisthopus*) that can be considered as such. Hence apparently the *humidity* of the oceanic climate also has a significant—positive or negative—role (see further remarks

*Of course the percentage of "autumn insects" in Larsson's "western group" is too high. His worst mistakes are inclusion of *Bembidion nitidulum* in the Pan-Scandinavian group, and of *Agonum assimile* in the eastern group.

on p. 485). Among the 11 "western" adult hibernators not one is markedly xerophilous.

The view that larval hibernation in a continental climate is unsuitable is strongly supported by Palmén's data (1946) based on records of immature carabids which were found in East Karelia. These are so strikingly late for a series of species considered as larval hibernators in Scandinavia that it must be assumed *that the species concerned must have partially or completely switched to adult hibernation in East Fennoscandia*. It is especially useful to study the data given by Palmén (mentioned in the Supplement of this book) for the following species: *Amara apricaria*, *A. aulica*, *A. brunnea*, *A. consularis*, *A. fulva*, *Calathus erratus*, *C. melanocephalus*, *Nebria livida* (immature beetles, June 18, but also August 22; "larvae in greater numbers during July"), *Trechus secalis*.

It would be very tempting—a task strongly recommended to some young, energetic entomologist—to undertake a comparative *experimental* study of the groups of western and eastern Fennoscandian Coleoptera (and other insects). Especially important would be an accurate study of the thermal responses of the larvae.

Further evidence that the difference of the northern limit in Fennoscandia between the "western" and "eastern" type is climatically determined can be provided by a study of the distribution in the rest of Europe. I have preferred
478 to investigate whether or not the species in question occur in Ireland, i.e. a pronounced oceanic area.

If the above three groups are taken we obtain the following results:

1. Among the 39 species that in *Finland* advance farthest north, 17 species, i.e. 44%, are missing from *Ireland* (*Acupalpus flavicollis*, *Agonum livens*, *Amara equestris*, *Amara montivaga*, *Badister peltatus*, *Bembidion andreae*, *B. articulatum*, *B. humerale*, *B. ruficolle*, *Cicindela hybrida*, *Dromius marginellus*, *Harpalus smaragdinus*, *Microlestes maurus*, *M. minutulus*, *Nebria livida*, *Oodes helopioides*, *Pterostichus angustatus*; *Carabus cancellatus* and *Dyschirius lüdersi* are doubtful). However, of these 17 species only 5 (*Amara montivaga*, *Bembidion humerale*, *B. ruficolle*, *Dromius marginellus*, *Microlestes minutulus*) are missing from England. Only for these might it be possible to argue that they could be missing from Ireland because of the immigration history, all the more so since none of the remaining 12 species is consistently flightless (*Microlestes maurus* is dimorphic).

2. Of the 35 species that also advance far north in Sweden but avoid the Norwegian west coast (at least in the north), 11 species, i.e. 33%, are missing from Ireland (*Agonum ericeti*, *A. quadripunctatum*, *A. sexpunctatum*, *Amara famelica*, *A. littorea*, *A. municipalis*, *Bembidion obliquum*, *B. quadrimaculatum*, *Cicindela silvatica*, *Dromius sigma*, *Tachyta nana*). *Amara littorea*, *A. municipalis* and *Tachyta nana* are also missing from the rest of the British Isles. These species, as well as *Agonum ericeti* and *Dromius sigma*, which are constantly or almost constantly flightless, may be missing from Ireland for dispersal capability reasons, but scarcely the remaining 6 species.

3. Among the 26 species whose area in Norway reaches the highest latitudes only 4 species, i.e. 15%, are missing from Ireland (*Amara ingenua*, *Carabus coriaceus*, *C. hortensis*, *Trechus secalis*). The first 3 species are entirely absent from the British Isles and the fourth species (*Trechus*) is constantly flightless. The absence of these 4 species from Ireland is certainly due to dynamic (historical) reasons.

Finally it may be mentioned that the 6 species that occur more or less isolated in the "warm region" of southeast Norway (p. 454) are all missing from Ireland, with the exception of *Abax ater*.

The above geographical comparison has shown that the more or less pronounced *eastern*—one might say *continental*—element of our "southern fauna" is also characterized in western Europe by avoidance of regions with a markedly oceanic climate.

479 C. Duration and Frequency Figures of Temperature

Early on, scientists thought of calculating the period during which the temperature exceeds or falls below a definite figure (mean, minimum or maximum), instead of expressing the biologically effective factors of climate by yearly, seasonal or monthly temperatures—i.e. the time factor is fixed while the temperature factor remains variable. *The temperature factor was therefore fixed* and a variable time factor was obtained. In this way the isotherms were replaced on the map by thermo-isochrones (see the historical account in Langlet, 1935).

Duration figures are required for a period during which the temperature *continuously* falls below or exceeds a certain level. If only the number of days in the year with a particular thermal characteristic is summed we get *frequency figures*.

Simple frequency maps are those reproduced above from Hamberg (1914) of the mean number of days with frost. Frequency values of mean temperatures were also compared by Samuelsson (1915), Rubinstein (1924) and Lunelund (1942b), with definite plant limits—especially the area limits of trees. The common isotherm maps for April + October or for May + September remind one of frequency or duration maps in their content, for they appear to provide an idea of the length of the vegetative period. But technically they are isotherm maps.

During the last two decades, Enquist (1924, 1929, 1933) seriously followed the frequency method and tested it on plants. He avoids the use of mean temperatures and proceeds consistently from frequency figures (which he calls "duration figures") of maxima and minima. With these he constructs thermo-isochrones which he compares with the area limits of forest-forming trees. To determine the frequency figure decisive for the species of tree concerned, Enquist (1933, pp. 151 ff.) proceeds as follows: He draws the frequency curves

of the maxima or minima of the year (mean figures for several years) for a number of stations located as close to the area limit of the species as possible. That is, he marks the number of days in the year on which a maximum (or minimum) temperature of $\pm 0, +1°, +2°C$, etc. is normally exceeded. When two such curves of stations, located along the limit of the plants species, intersect, this indicates that the frequency value represented by this point is common to
480 the two localities. With this procedure Enquist claims *to have automatically found the decisive area-limiting factor for the plant species in question*. He is misled (1933, p. 207) into such categorical statements as: "For the spruce to grow spontaneously, the maximum temperature must reach at least +12.5°C on altogether 65 days."

No wonder Enquist's conclusions were seriously contested by a number of biologists. His method has been subjected to severe criticism, foremost by Langlet (1935), whose reasoning, it seems to me, is largely sound. A. Hamberg (1924), Almquist (1929, p. 22), and Lindroth (1939, pp. 244–245) have also been reluctant to accept Enquist's view.

To me the following seem to be the main objections to Enquist's procedure:

1. The maxima and minima of temperature that he uses are likewise *mean values* and consequently not "factors," but constructions. Of course it must be conceded that these represent only "mean values of the first level," i.e. the figures were obtained by simple calculation from the figures for a number of years. They are therefore less balanced than the mean monthly minima that I used above (Figs. 64–69), which represent "mean values of the second level" whereas the mean temperature for a month (for example, Fig. 63) even signifies a "mean value of the third level": First the mean was calculated for each day, then for each July, and finally for the sum of all the July months in the series of years studied.

But, to arrive at a view as to the extent of variation of the frequency values expressed by thermo-isochrones—the "mean values of the first level"—in different years, I selected eight stations in widely separated parts of Sweden and for each year during the period 1919–1943 I expressed the frequency of the days with a minimum temperature > ±0°C (i.e. of frost-free days) by curves (Diagram 49; Table 32). This temperature factor was used by Enquist to explain the area of both *Pinus silvestris* (1924, p. 207) and *Picea excelsa* (1929, p. 21). A similar curve is given by Hjelmqvist (1940, p. 195) from Bergen in Norway for maximum temperatures > 18°C over more than 60 years.

481 The 25-year period shows an astonishing variability in the frequency values and the mean value is clearly a construction. The long continuous series of years (up to 8 years) with minus values is especially critical. How does the plant or animal behave if its minimal requirements of the decisive "factor" are not fulfilled over such a long period? It must be conceded that of all organisms, trees must be able to survive such adverse periods the best. It might be possible

Table 32. Frequency of days with frost and frost-free days at 8 Swedish stations, 1919–1943. Cf. Diagram 49

	Average number of days with minimum $> \pm 0°C$	Amplitude of days with frost	Mean deviation from average	Years with largest number of minus values	Years with largest number of plus values
Malmö	279	39–133	21 days	3	3
Halmstad	273	46–145	19 "	4	4
Visby	272	44–154	21 "	3	5
Västervik	255	78–172	16 "	8	3
Stockholm	245	83–168	17 "	8	6
Harnösand	192	136–209	14 "	7	3
Haparanda	170	165–223	12 "	4	4
Karesuando	134	209–253	9 "	4	3

to assume that the "factor" primarily influences their reproductive capability, seed formation, ability of seed germination, growth of the young plants, etc. They might be able to survive for several years without or with greatly reduced mutiplication. It is known that seed formation in conifers in certain years may fail completely in large areas without seriously endangering the forest stands.

But if trees (and other perennial plants) actually occupy a special position, in that they are able to survive long periods with negative deviation from the mean value of the "factor," it follows *that Enquist's "duration figures" cannot be applied to annual and biennial plants or to animals that must reproduce every*
483 *year, and so cannot be used to explain the area limits thereof.*

2. The procedure described whereby Enquist hopes to be able to find the decisive frequency value for a species of plant is unreliable. He even states emphatically (1933, pp. 152, 195), that the frequency value sought can be "sufficiently determined from just two stations," i.e. that it is directly derived from the point of intersection *of only two* frequency curves from stations situated at the area limit (in this case at the birch limit). This idea is understandable only on Enquist's assumption that the factor sought must be found among his frequency values. But the objective researcher would have first sought confirmation of his theory *in the intersection of several curves*. Langlet (1935, p. 347), who constructed frequency curves for a large number of stations near the timberline, failed to establish the regularity posited by Enquist.

3. It is wrong to take only *marginal values* as Enquist does. It cannot be inconsequential for organisms whether, for instance, 200 frost-free days include a pronounced or a poor midsummer period. At least as important as the frequency values is the *optimum* temperature. The longer the part of

summer close to that temperature, the shorter the time required by the plant or animal to complete the life process necessary before over-wintering. An idea of the optimum temperatures is best obtained from mean temperatures. We learn better the life requirements of the organism if we work both with the minima in spring and autumn and with the midsummer mean temperature.

4. Enquist's thermo-isochrones show greater detail than is possible from the density of meteorological stations (for example, 1929, p. 21, Fig. 9, North Sweden; 1933, p. 157, Fig. 7). Their correspondence on the map with one or other treeline is thus no proof of a causal relationship (emphasized by Langlet, 1935, for instance, on p. 351).

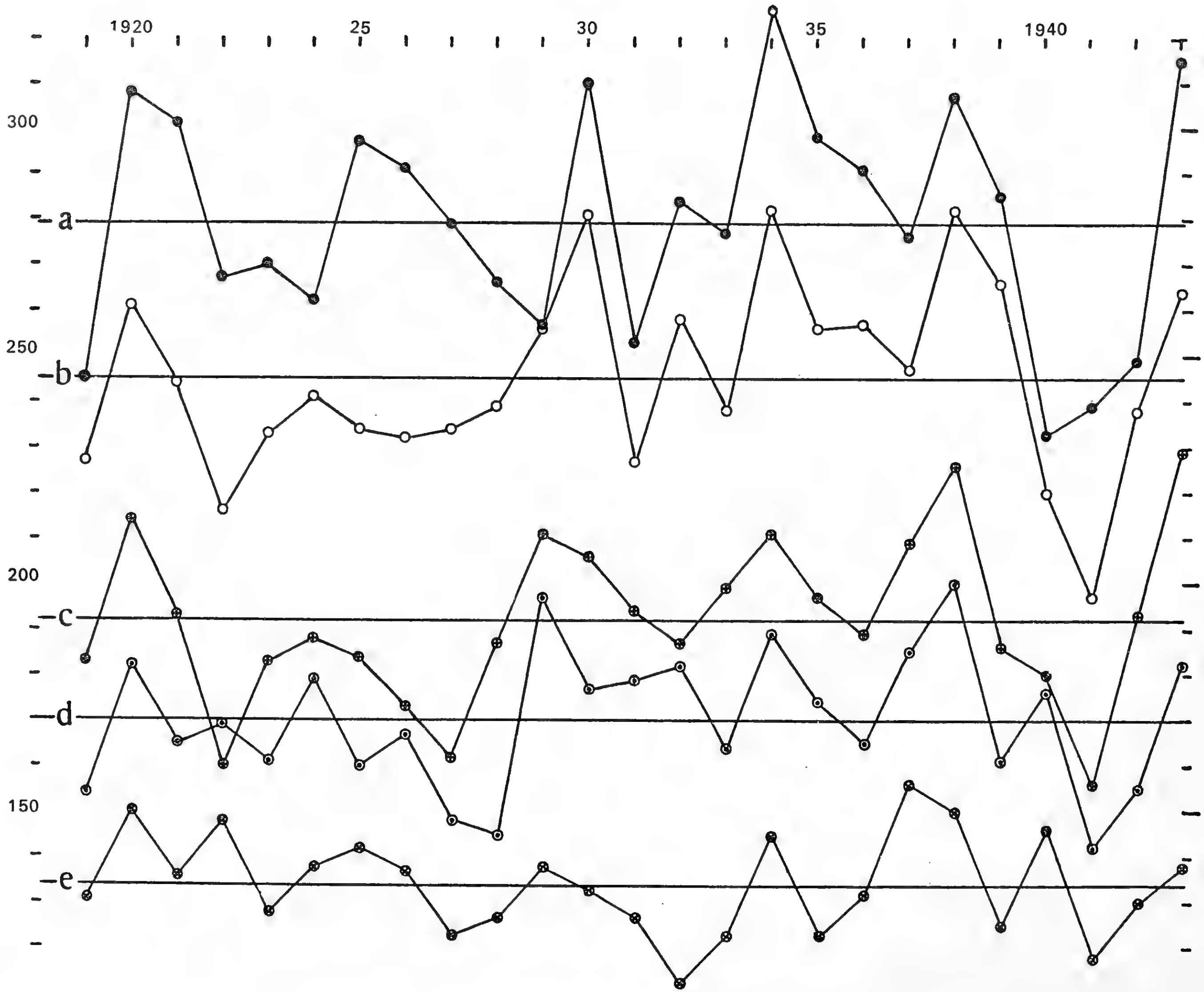
5. The meteorological stations Enquist uses (for example 1933, p. 151) are
484 not directly comparable because they only partially cover the same periods of time. How important this is in view of the large climatic changes during recent decades is evident from the diagrams given below (pp. 644 ff.). By reverting to some of the frequency values Enquist gives to the same period of the year, Langlet (1935, p. 345) found that they came out reversed for two stations (Kiruna, Storlien). Comparison of the frequency of frost-free days according to the older figures on Enquist's map (1924, p. 207, Fig. 5) and the figures given above (Diagram 49; Table 32) for the period 1919–1943 likewise reveals considerable differences.

6. All Enquist's frequency values were taken from meteorological stations. They therefore show the *macroclimatic* conditions. How little these are to be considered as biologically effective factors will be shown in a subsequent section (p. 498). And, it is just the maxima and minima of temperature that are strongly affected locally, not the media.

On the other hand it must be conceded that forest trees, which are Enquist's main concern, are of all living beings the ones in closest contact with the macroclimate, since they grow high and are less influenced by the winter snow cover (Wegener, 1923). But it must be determined whether even for forest trees the germination and growth of young plants do not represent, climatically, the most sensitive time of life. If they do, trees are also influenced lococlimatically and microclimatically to the extent that the usual meteorological data, *as they are treated,* are completely inadequate.* This must be decided by purely biological observations and experiments on the various stages of trees.

In conclusion, concerning Enquist's procedure it may be stated that his thermo-isochrones can in some cases—perhaps just for forest trees—provide a better expression of the climatic requirements of a plant than the isotherms of monthly averages, monthly minima, etc. But, and this is a serious objection, they can never express anything more than that, since for one species of plant a

*I am unable to judge whether the limits of the pine and spruce area actually *climatically* determined in all directions, as claimed by Enquist (cf. Langlet, 1935, pp. 357 ff.).



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mild summer is especially important for life, for another midsummer heat, for
485 a third a long enough vegetative period, etc. Enquist's big mistake is that he claims to have found the one decisive area-limiting factor, which is impossible. In principle his line of thinking signifies an advancement, but he has caused more damage than good, the more so since his "theory" was received with great enthusiasm not only by geographers and people generally interested in nature, but even by several outstanding botanists, who should have known better. It is accepted as fact in Swedish grammar-school textbooks of geography (for example, Swedberg, 1931).

Hjelmqvist (1940), a faithful follower of Enquist, extended the procedure in the right direction by working experimentally with the plant concerned (*Fagus silvatica*). He expresses himself more cautiously than Enquist, though still not cautiously enough, when he attempts to determine the decisive factor for a certain section of the area limit (for example, pp. 169 ff., 185, 193 ff., 207, 229, 236). But it is strange that Hjelmqvist does not seriously discuss the objections raised by Langlet (1935) and others against Enquist's method.

Precipitation and Humidity

The precipitation in Fennoscandia is so unevenly distributed (Fig. 73) that its biological effect, if any, cannot but be evident. Generally speaking, there is a fairly regular decline going from the west, where on the Norwegian west coast several regions exceed 2000 mm per year, to the east, and to a lesser extent from south to north. The lowest figures (< 400 mm) occur in three less extensive regions: in the southernmost parts of Öland and Gotland, in parts closest to the coast of Vbt and Nbt, and in the inland of the Far North. Also of particular interest are two isolated regions: a deficit region in the inner valleys of eastern south Norway, where the annual precipitation remains below 600 mm and an excess region in the western part of the south Swedish highland, which in part receives more than 1000 mm.

487 If we wish to evaluate the zoogeographical consequence from the distribution of precipitation we must be clear whether the yearly (mean or absolute) amount of precipitation can really be considered as a biologically effective factor. This factor might be *negatively* effective, and in the case of insects in such a way that definite "flying animals" are hindered in the flight effectiveness, essential for life. In this connection the fairly regular decline of Lepidoptera in

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482 Diagram 49. Number of frost-free days at 5 Swedish localities, 1919–1943. Compiled from "Sveriges Meteor. u. Hydrol. Inst Årsbok" (1919–1943).

a—Malmö; b—Stockholm; c—Harnösand; d—Harparanda; e—Karesuando. Horizontal lines are mean figures at each locality during period. Cf. Table 32.

Europe toward the west is conspicuous (Pagenstecher, 1909, pp. 15–16; Heydemann, 1930). It has been partly ascribed to the increased precipitation. But since the phenomenon especially affects butterflies† it is uncertain whether or not the lack of sunshine represents the more important factor (Lindroth, 1931, p. 393). In heavy, continuous rain, soil animals can also naturally be endangered by more or less local floods. In our climate, where the precipitation is fairly uniformly distributed over the whole year, this danger is comparatively slight.

At any rate the annual precipitation can never be considered as a *positive* biogeographical factor by itself. It is therefore advisable to take into consideration its two most important results (a third, the insolation, is separately dealt with below on p. 495). These are the ground moisture and the humidity of the air.

The *ground moisture* is of course actually an edaphic characteristic. But since it may be primarily dependent on the precipitation and evaporation, and only incidentally (in our region) on the drainage conditions, it seems justified to consider it under climatic factors.

In Fennoscandia there are only a few extensive regions uninhabitable for a number of species because of *insufficient* ground moisture. The most important are the alvar regions on Öland and Gotland and the heaths of the fjelds. But in the latter the cold factor is more detrimental. Nevertheless, a species cannot be excluded from an entire province only because of insufficient ground moisture. The gaps due to that are scarcely noticeable on the maps of Fennoscandia, so this negative factor has on the whole no zoogeographical significance.

The condition is different in regions that show an excess of ground mois-
488 ture. We are not thinking here of local moor and other swampy regions formed by poor drainage conditions, but of the regions with the heaviest precipitation, meaning Norway west of the main Scandinavian watershed. In the above treatment of the more or less pronounced eastern species, which clearly avoid these regions of Norway (p. 462), we found a large degree of correspondence with the development types, where the species, with few exceptions, are adult hibernators (p. 476). Species that prefer western Scandinavia (p. 474), are predominantly larval hibernators. The exceptions are:

a. Eastern species hibernating in the larval stage:

Amara equestris
A. fulva
A. municipalis
Broscus cephalotes
Cincindela hybrida
C. silvatica
Harpalus smaragdinus
Nebria livida
Pterostichus lepidus
P. vulgaris

†(which are diurnal; suppl. scient. edit.).

Synuchus nivalis	*Trechus quadristriatus*

With the exception of *Nebria livida* (but also see p. 477) and *Pterostichus vulgaris*, these species are more or less pronounced *xerophilous*.

b. Western species hibernating in the adult stage:

Agonum assimile	*Bradycellus collaris*
A. ruficorne	*Dromius quadrinotatus*
Amara ingenua	*Pterostichus strenuus*
A. lunicollis	*Trechus micros*
Bembidion femoratum	*Trichocellus placidus*
B. nitidulum	

None of these species shows xerophily.

We may therefore conclude that the faunistic differences between west and east Fennoscandia—apart from factors related to the immigration history—are due not only to the thermic factors discussed above (pp. 474 ff.) but also to the humidity. That is, numerous markedly xerophilous animals cannot survive west of the main Scandinavian watershed. It is not possible to decide without experimental study of the species concerned whether the high moisture of the soil or humidity of the air play the main negative role.

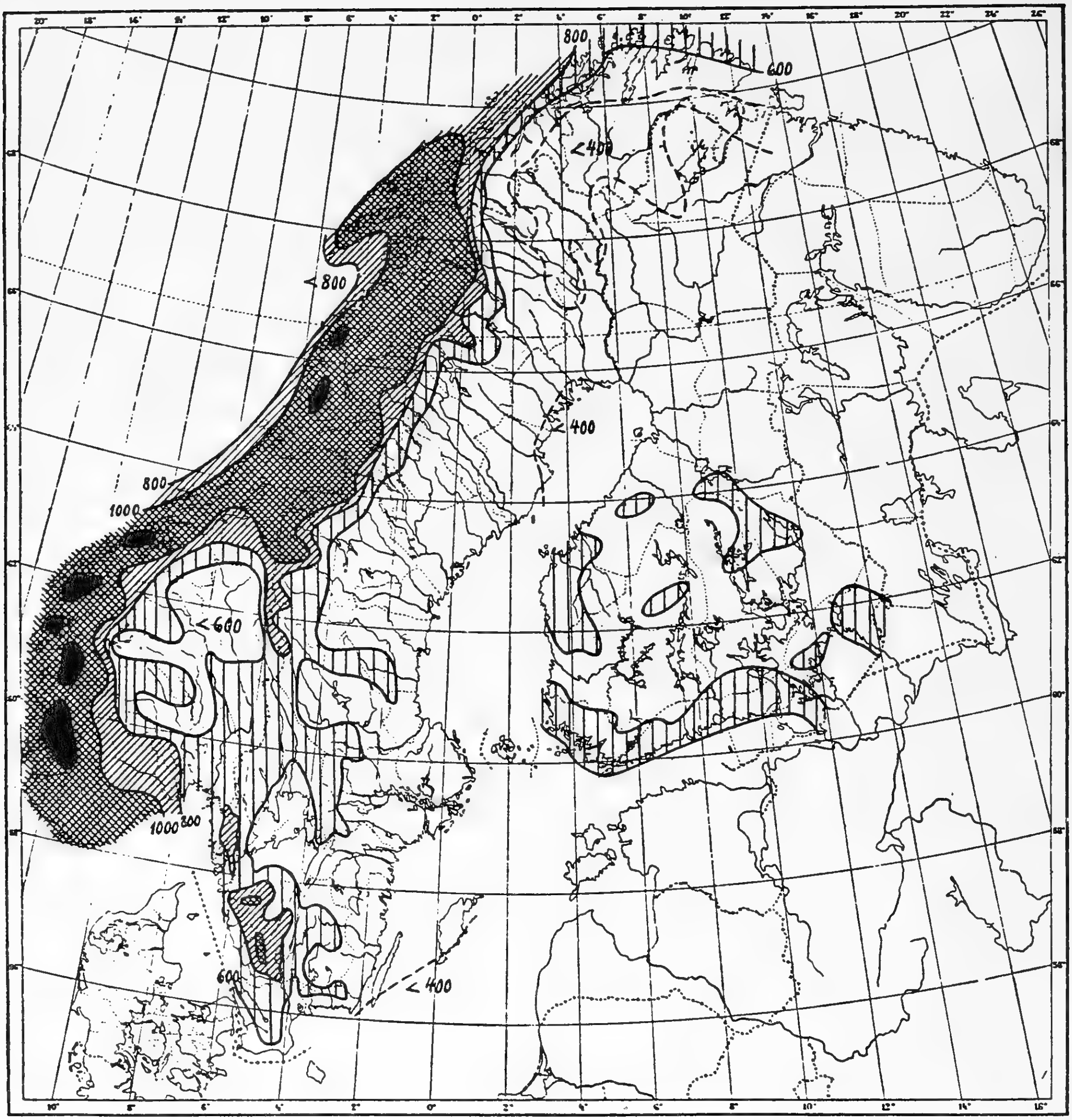
Such a study would certainly be worthwhile. In any case a glance at the
489 map, for instance, of *Amara fulva* shows that the western limit of this flying species cannot be due to dynamics.

Humidity of the air can be expressed as an absolute or as a relative quantity. Wallén (1930, p. 33) published maps on the absolute humidity of the air in Sweden for January, July, and the whole year. It is not a biologically effective factor.

Relative humidity of the air, according to the same author (l.c., p. 34), shows differences between different parts of the country that are too small for cartographic representation. On the other hand the daily fluctuations are too large.

The great dependence of the humidity of air and moisture of the ground on temperature and the difficulties of expressing the former of these directly on the map have led many researchers to construct climatic indices in which both precipitation and temperature are represented.

One understands the motive, for example, to express the reduced evaporation of the precipitation in cooler areas. This is done in the simplest way with Martonne's humidity figures (Hesselman, 1932) = annual precipitation: (mean temperature of the year + 10°C). These figures show the proportion of precipitation that—with identical drainage conditions—reaches the soil (although the French "humidité" and the English "humidity" are the same as humidity of the air). In a region the size of Fennoscandia, where the temperature differences are not very large, the humidity map (Fig. 74) will on the whole coincide with the precipitation map; in the southern half of the



486 Fig. 73. Mean distribution of precipitation in Fennoscandia. From "Nedbøriaktt. i Norge" (1938), Ångström (1946), *Atlas öfver Finland* (1910). Black area = > 2000 mm.

region this is especially evident. The mean—theoretical—ground moisture, as an expression of an area-limiting factor, has little significance.

Among other ways of determining the humidity of the climate, mention may be made of A. Meyer's (1926) "precipitation-saturation deficit quotients," i.e. *precipitation : saturation deficit*. The latter is calculated from the mean values (of the year and of individual months) of temperature and relative humidity of the air put out by the meteorological stations. Heydemann (1930) in his study of the dependence of the lepidopteran fauna of Schleswig-Holstein on the Atlantic climate, used Meyer's N-S quotient maps. But according to Hes-
491 selman (1932, pp. 524 ff.), who tested the method empirically for two Swedish stations, the saturation deficit calculated by Meyer is beset with such large errors that for Sweden he preferred to use Martonne's humidity figures.

As discussed above (pp. 462, 474), the oceanic (Atlantic) climate is marked not only by high humidity (of the air as well as of the ground) but also, equally, by thermal conditions. It is natural to attempt to express the "oceanicity" of a region by a single index value, taking into account both groups of factors. The attempt was made by Kotilainen (1933) with an "oceanicity index" calculated as follows:

$$\text{Oceanicity index} = \frac{\text{yearly precipitation} \times (a - b)}{10 \times (T_1 - T_2)}$$

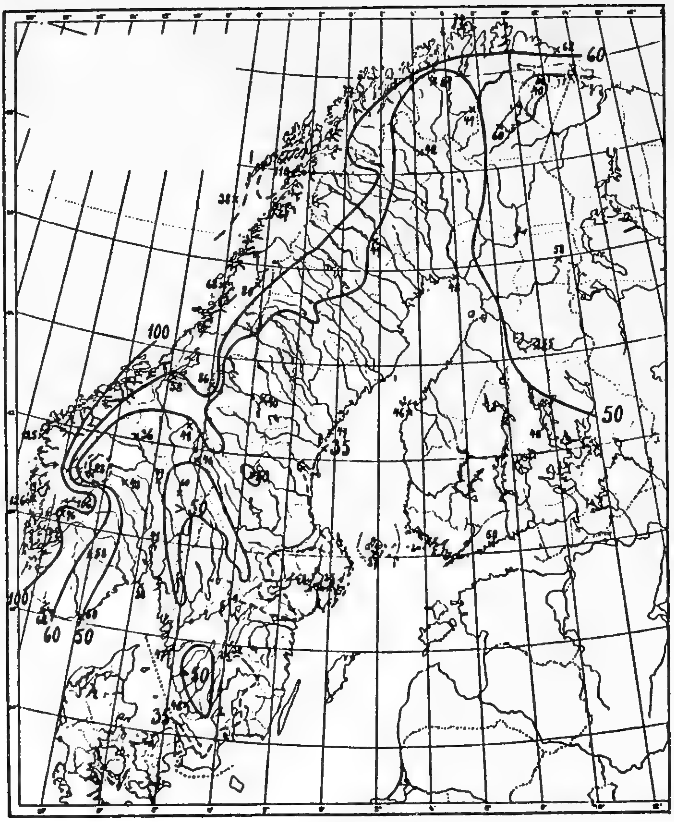
where a = number of days with mean temperature > ±0°C;
b = number of days with mean temperature > +10°C;
T_1 = mean temperature of the warmest month;
T_2 = mean temperature of the coldest month.

Supplementing Kotilainen's data (p. 56) with further indices for Norwegian and Swedish stations, I have constructed a new "oceanicity map" (Fig. 75).

Although it is evidently important to be able to determine whether a particular area limit of an animal or plant species is determined either by thermic or by hygric factors, I believe that Kotilainen's oceanicity is not without interest. Attention may be drawn to the low figures of the Oslo region (*Nebria salina*), to the eastern interior of south Norway, and to the comparatively high figures of Visby on Gotland (*Nebria salina*, *Trechus obtusus*). At the least such a map, taken with the "pure" maps of temperature, precipitation, etc., can contribute to a judgment as to whether a particular area limit *can* be existence-ecological or not.

Finally mention may be made of Cook's (1924) *Climatograph.* It is a simple and practical method of combining into *one* diagram thermic and hygric factors (mean temperatures and quantities of rain each month) at a number of places within the area of the species of animal concerned.

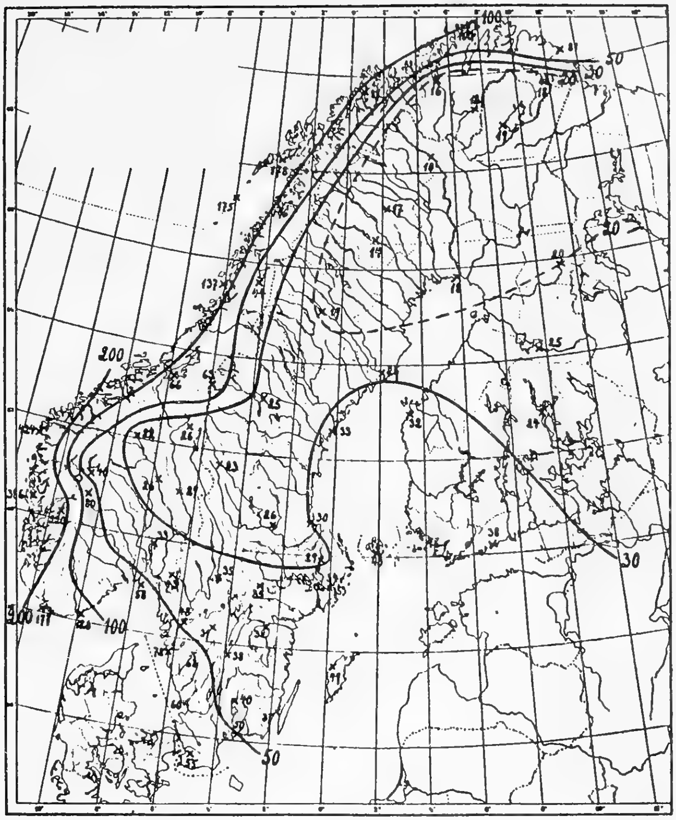
The strong effect of humidity, not only of the ground but also of the air, can be ascertained more easily in the case of *plants* than of animals. Degelius
492 (1935, pp. 244–270) thus clarified the close association of the "oceanic" lichens



490 Fig. 74. Martonne's humidity figures. After Hesselman (1932), supplemented from Kotilainen (1933), "Nedbøriaktt. i Norge," 42 (1938), and "Norsk Meteorol. Årbok" (1946).

with the Scandinavian regions having the highest precipitation. He rightly considers the hygric factors of climate more important for these plants than the thermic factors. Earlier, Hård (1924, pp. 147, 225) gave a similar account of the western species of the flora of south Sweden.

That any comparable dependence of *animals* is so obscure is due to many factors. First, animals are not so dependent on the occurrence of free water for the intake of food and for their metabolism. Second, unlike the higher plants, they are not bound to a locality. If there is danger of desiccation they can save themselves by hiding in the ground, flying away, etc. And they can search for water, to replace by drinking, any loss caused by transpiration.



490 Fig. 75. Kotilainen's (1933) "oceanicity index". Supplemented from Hamberg (1922), "Nedbøriaktt. i Norge", 42 (1938), "Norsk Meteorol. Årbok" (1946) and official Swedish meteorological data.

The experiments with insects in which the humidity factor was operative show the more or less strong response to loss of water in all species, most of all, naturally, in distinctly hygrophilous species. As the transcript of experiments (pp. 78 ff.) shows, in some cases this response is stronger than that to the thermal effect. From this it must be concluded that the humidity of the air, in nature, represents a decisive factor for these animals too, and is probably the most important climatic factor along with temperature. The difficulty in clearly determining its effect in the field, in the habitat of the animal, or from its distribution map, is due not only to its mobility but also to the common *micro-stratification* of air of diverse humidity in *and on the ground* (for example, Geiger, 1942, pp. 88 ff., pp. 275 ff.). As long as the conditions of

relative humidity of the air cannot be represented on a map, it rarely plays a decisive role for the general distribution of insects. In regions where a certain minimum requirement of humidity of the air is nowhere fulfilled—in deserts and steppes—or where the air is almost constantly saturated—in an extreme oceanic climate, in tropical rain forest—certain species can be ruled out for these reasons. Moreover the humidity of the air is a *microclimatic factor* of the first order. This therefore determines the habitat of the *individual* rather than the area of the *species*.

For this reason the humidity of the air in our climate is more an *ecological* than a *zoogeographical* factor. A phenomenon to which I have drawn attention
493 in connection with the fauna of Iceland (Lindroth, 1931, p. 387) is the tendency of the more or less pronounced forest species in the rainy climate of western Europe to inhabit more open ground, sometimes drier places than normal. The explanation for this "ecological adaptation" must be that in such regions, even in an exposed situation, both air and ground possess sufficient humidity. Of the three carabids (*Notiophilus biguttatus*, *Patrobus atrorufus*, *Trechus rubens*) especially mentioned from Iceland, the same ecological change applies at least to the *Patrobus* species in West Jämtland. From west Norway, where this phenomenon is expected to be most pronounced, we unfortunately possess all too little authentic ecological collection data. However, the strikingly high percentage of "forest species" in the fauna of Hitra and the adjacent islands (p. 320), all of which are almost devoid of forest, seems to me explicable only in this way.

The combined effect of thermic and hygric factors determines the duration and depth of the *snow cover*. This plays an important role by insulating the ground thermally against low air temperatures (Geiger, 1942, p. 159). Whether at −20° or at ±0°C, the ground temperature can remain almost unaltered if there is a deep snow cover. Instructive figures were obtained by Keränen (1920, pp. 52–53) from measurements taken in Lk Sodankylä. During one December month the mean temperature of the air was −24.4°C, but on the ground only −6.5°C under a snow cover averaging 32 cm. During October 1916, in the absence of snow, the mean temperature was: air 4.3°C, ground −2.1°C. During December of the same year, with 32 cm mean snow cover, it was respectively −11.1° and −1.4°C. Soil organisms susceptible to cold will thus be adversely affected by *frosty days when ground is bare*.

I therefore have attempted to calculate the mean number of such days for different parts of Sweden. Exact data for different sections have never been published, but an isochrone-map on the mean number of frosty days is given by Wallén (1930, p. 21), and I have obtained a corresponding, unpublished map on the average duration of snow cover (1909–1935; in simplified form in Ångström, 1946, p. 48) from "Sveriges Meteorol.-Hydrol. Institut". From these two maps it is possible to estimate roughly the mean minimum number of frosty days with bare ground for any locality in Sweden. With the exception

494 of the region west of Torneträsk in Lapland the number of frosty days is everywhere greater than the number of days with snow cover. The difference—i.e. the minimum number of frosty days with bare ground—is largest in the frontier region between Skåne and Småland: about 110 days. The figures show such an irregular distribution that preparation of an isochrone-map on the basis of the available material proved to be impossible. (A map on the average date of the thaw in different parts of Sweden has been published by Edin, 1941, p. 33.) The north, especially the fjeld regions, has the smallest number of frosty days with bare ground. In the south the west coast has somewhat higher figures than the east coast.

If we can establish a regionally determined gradation of the number of frosty days with bare grounds on the basis of a thorough consideration of the figures of every station, this undoubtedly represents a significant biogeographical factor. However, it is more probable that it will turn out to be mostly locally (lococlimatically) determined, so that it influences more the local than the general distribution of organisms.

Other Climatic Factors

For regularly flying insects the *wind conditions* constitute a decisive environmental factor. For such insects the wind is not only an important mode of dispersal but can also be decidedly area-limiting in very exposed regions, especially in regions without forest. This is clear in the case of Lepidoptera (Pagenstecher, 1909, p. 16; Hesse, 1924, p. 555), in Scandinavia especially in the Alvar regions in Öland and Gotland (Wahlgren, 1917, p. 53), in the *regio alpina* of the fjelds, and on the outer naked rocky skerries, chiefly at the Norwegian coast.

The importance of wind as a mode of dispersal for Carabidae is considered elsewhere (p. 573). This factor may possess an *area-limiting* effect only in exceptional cases. Very few carabids (*Cicindela*; *Bembidion*, subgenus *Bracteon*; see p. 579) fly so regularly as to be seriously endangered at places exposed to strong winds. Probably the fact that *Bembidion lapponicum* and *B. velox* in Norway avoid the outer coastal belt can be attributed to the deleterious effect of the wind. However, this does not seem to be so in the case of *Cicindela campestris*. The above species are also heliophilous, which probably has at least as important an area-limiting role.

495 The main reason for attributing little importance to the effect of wind as an area-limiting factor for carabids is the composition of the insular faunas, considered above (pp. 198 ff.) in a separate section. It was shown that even the fauna of woodless islands such as Helgoland (p. 328), which have been exposed to wind for thousands of years, has not undergone perceptible change in the direction of an increase in flightless species and forms.

While some carabids, especially the species with metallic color, are

markedly heliophilous, it is fairly probable that right from the beginning the *insolation*, the number of sunny hours, was an effective climatic factor. We are not dealing here only with the effect of light. Apart from the fact that the insolation of a locality is determined indirectly by decrease in fog, precipitation and similar factors, and thus provides a kind of converse index of their extent, it is a *thermic* factor of the first order. This seems to be all the more significant inasmuch as the usual meteorological measurements take the temperature in the shade. It is actually difficult to decide whether the sun influences heliophilous animals more as a light factor or a thermal factor (and so indirectly as a humidity factor). Probably, for most species, the purely thermic effect is the more important.

Anyway, a map of the average number of sunny hours—best taken over the summer half-year—must be important just from the entomogeographical viewpoint (Fig. 76). A comparison with the isothermic map for July (Fig. 63) and for the other relevant months (for example, Hamberg, 1980; Ångström, 1946) shows that high air temperatures in the shade are not always associated with strong insolation. Instructive in this connection is the Mälar region, thermally the most favorable part of Scandinavia at midsummer, which is rather poorly insolated at that time (further information for every month was provided by Hamberg, 1909).

Some interesting details of the "insolation maps" are considered below:

1. By far the sunniest region of Scandinavia is *Gotland* (probably, for lack of stations, Öland comes off with low values). As a result the otherwise favorable thermal conditions of the island are considerably enhanced, which further explains the strikingly southern character of the fauna (pp. 289 ff.).

497 2. The frontier region between Norway and Sweden east of the *Oslo fjord*. Markedly heliophilous species, such as *Amara montivaga* and *Lebia cyanocephala*, might be favored here. Some places in the inner eastern valleys of south Norway, and at the inner end of the Sogne fjord, also show high figures, which help to explain the thermophilous faunal element considered earlier (p. 454), including some of the xerophiles, here far advanced.

3. Regions of the northern end of the *Gulf of Bothnia*. At midsummer the number of sunny hours here is relatively even higher than shown on the map. A whole series of more or less heliophilous species here find their northernmost area limit and/or occur with frequency and in abundance, for example:

Agonum dolens	*B. quadrimaculatum*
A. piceum	*Carabus clathratus*
A. versutum	*Harpalus aeneus*
A. viduum	*Pterostichus coerulescens*
Bembidion obliquum	*P. lepidus.*

The same is true of the following non-heliophilous species:

Cymindis macularis	*Dromius longiceps*

D. sigma *Synuchus nivalis.*
Lebia crux-minor

Nevertheless, they may be thermally favored at sunny places. This is especially probable for *Dromius longiceps* and the *Cymindis* species, which live on dry sand slightly warmed by the sun. Likewise we may notice the species mentioned earlier (p. 462) that occur more or less isolated in these regions (*Chlaenius nigricornis*, *Panagaeus crux-major*, *Pterostichus vernalis*). The genus *Chlaenius* is markedly heliophilous.

Three species show a very revealing distribution:

Agonum sexpunctatum *Metabletus truncatellus.*
Cicindela silvatica

They not only show, like the above, a strikingly rich occurrence north of the Gulf of Bothnia, but they *retreat* in Jämtland, where they do not reach the region of Storsjön. Also in Norway they are markedly eastern, but two of them (*Agonum*, *Metabletus*) reach the inner Sogn (cf. p. 454). It is clear that they avoid a markedly oceanic climate. But which of these factors is
498 decisive: the cool summer, high precipitation and humidity of the air, or lack of sunshine? All three species are pronouncedly heliophilous, two are also clearly xerophilous, but the third species, *Agonum sexpunctatum*, is hygrophilous, and at least for this species the humidity factor may be excluded. In Lapland the species extends far beyond the 15°C isotherm for July, which in Jämtland falls close to its limit, so its absence from the higher parts of the province does not seem to be explained by the insufficient summer heat. On the contrary *Agonum sexpunctatum* might *represent the best example of a species whose area to the west is limited by deficient insolation*. Strikingly, in the British Isles it occurs only in England.

Finally it may be mentioned that I tried—of course with a negative result—to test the resistance of individuals of one and the same species (and population) with different intensities of metallic coloration to the effect of direct sunlight. An unusually colorful series (from black to pale green) of 18 individuals of the highly variable *Harpalus aeneus* (Upl Värmdön, July 3, 1941) was exposed to direct sunlight in a large glass bowl. The carabids were then removed and numbered in the order in which they were affected by thermal paralysis of the hind legs. No correlation could be established between the coloration and resistance (not even according to sex); the longest-lasting specimen was a black male with a very slight blue shade.

On Lococlimate and Microclimate

Let us come back to the observations at the beginning of this chapter.

All the climatic factors mentioned so far and cartographically depicted are of *macroclimatic* nature. It is of course possible that some isolates, for

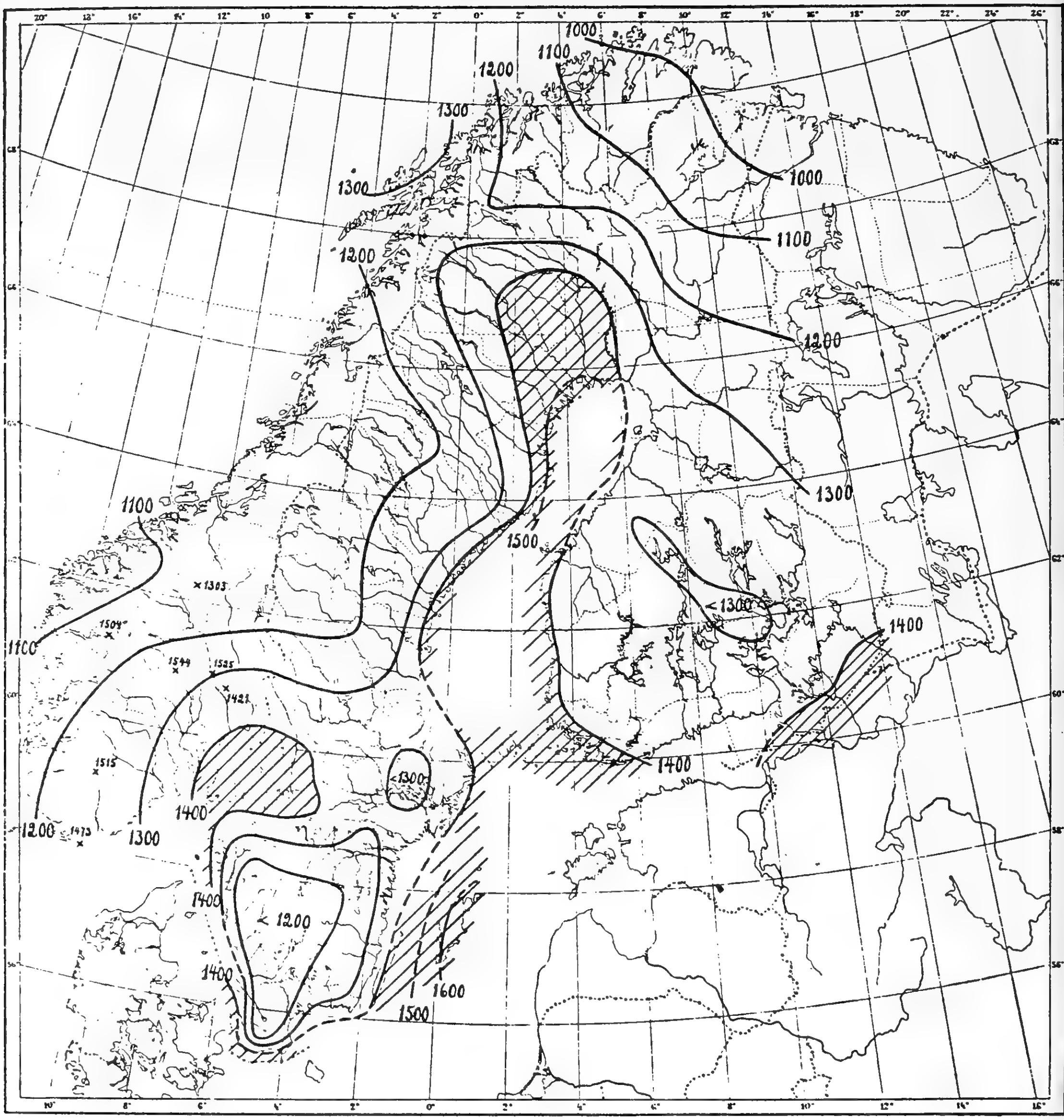


Fig. 76. Mean number of sunny hours during the summer half-year (April through September).

According to Hamberg (1909) and Lunelund (1942). "Isohels" are strongly generalized. Some Norwegian stations with abnormally high figures are indicated.

instance, the small thermal terrains in Norrland on the July isotherm map (Fig. 63), are actually lococlimatically determined, i.e. they reflect the placement of the instrument on an extreme surface. This could happen unintentionally, since meteorological measurements are generally considered representative for larger regions.

However, in general the usual meteorological figures are clearly macroclimatic, and in most contexts this is an important advantage. Their dependence
499 on the local conditions at the station is surprisingly slight. In considering the climatic changes of the last decade Ångström (1938, p. 26; original in Swedish) states: "The very uniform temperature fluctuations of different stations further support the claim already made that the figures of the monthly averages incorporate no errors arising from location and poor protection from radiation, etc. that exceed a few tenths of a degree." I made the same observation while studying the later climatic variations (p. 643). The minima (chiefly the absolute) and the precipitation figures might show a somewhat higher local variation.

The representative character of the meteorological climatic measurements, chiefly due to placement of the apparatuses an average 1.5–2 m off the ground, is an acute disadvantage from the biological point of view. The flora and fauna of the *ground* are exposed to very different climatic factors, which should be measured in the environment closest to the organism studied. A devastating insight into the unending fluctuations and deviations from the macroclimate of the "climate of the air layer next to the ground" is provided in the well-known contribution by Geiger (1942). The "discoverer" of the microclimate, Krauss (1911), provided plenty of convincing measurements. Concerning the investigation of the lococlimate and microclimate in relation to entomological materials, see Uvarov (1931, pp. 128 ff.), Franz (1931, 1933) and Kühnelt (1933, 1934).

Just one example that I have already given (Lindroth, 1943a) may be mentioned here since it illustrates with unusual clarity how big the thermal difference between adjacent and apparently similar surfaces can be. Two sampling plots were taken on and near the shore of a small lake in Upl Djursholm at a distance of 113 m from each other. On a July day the temperature of the air, at the soil surface, and at a depth of 5 cm was continuously measured. The curves of the temperature of the air were as good as identical, but those of the soil (Diagram 50) differed so much that *the maximum temperature of the "cold" plot (19.7°C, 1800 hours) did not reach the minimum temperature of the "warm" plot (19.8°C, 0600 hours)*.

It is therefore clear that the characteristics of the microclimate can never be depicted by a *cartographic* representation. Investigation thereof is a task
500 for ecology. But the biogeographer must never forget that, although the lines on the map that he uses to "explain" the area of distribution all concern the macroclimate, the *effective factors are always microclimatic*. On the map he is

working not with factors but with constructions, which suffer from a two-fold error: *They are mean values and they do not represent the true environment of the organism studied.* Hence even a perfect correspondence between a climate line and an area limit *should never be taken to prove more than that the limit is*
501 *determined by one factor (or more) lying within the climatic domain represented by this line*, for example, by the summer warmth, the length of the annual period of life, the humidity of the air, the insolation, etc. To avoid misunderstandings, in the present contribution I offer no area map indicating climate lines. My earlier contention may not have been too pessimistic: "In fact we will never succeed in cartographically representing the decisive climatic factors for an animal or plant species" (Lindroth, 1939a, p. 245).

Perhaps in the future we may deepen our understanding of the climatic conditions necessary for the life of animals and plants, apart from the insight obtained by microclimatic measurements, by using the "middle way," even if not the "ideal way," of the *lococlimate*. Here Krogerus (1937) has led the way with his temperature and humidity measurements on the south and north shores of the Paanajärvi Lake (Ks). I believe similar, extended investigations of the so-called southern mountains in northern Fennoscandia can yield good results, as already shown to a limited extent by Frödin (1915). The measurements should be taken in sequence with instruments placed close together (100 m or less) in extremely different positions, and the temperature and humidity of the air recorded at the usual height (about 1.5 m off the ground), in the air layer next to the ground and in the ground itself. Regional temperature measurements in the water close to the shore of different lakes would also provide a valuable clarification of the thermal conditions, particularly in the case of terrestrial and semiaquatic shore fauna.

The limnologists and oceanographers are generally in a more favorable situation. For them the air is replaced by water, which has a much more stable character.

Indirect Evidence of Climatic Factors

Without directly comparing the area of distribution of animals and plants with different climate lines it would be possible to undertake a parallel study thereof with biological manifestations of another kind which *must* be climatically determined, apparently showing the areas to be climatically determined too. *Phenological* observations are especially suitable for this purpose. They have been carried out in the Nordic countries since time immemorial, especially on the annual course of development of the more common species of plant. Some observations have been published.

Examples of this kind of parallelization are Siivonen's comparison (1942)
502 between the growth of *Bombus* species and the arrival time of the cuckoo (*Cuculus canorus*) in spring, and the calculation of the mean flowering period

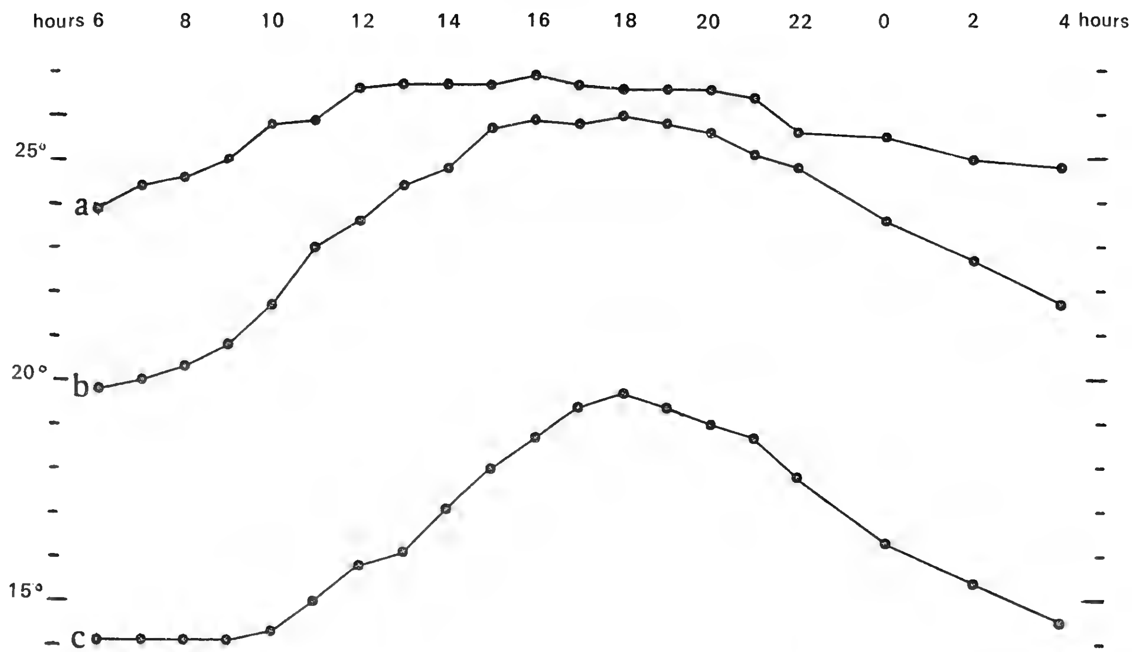


Diagram 50. Day-curves of temperature at depth of 5 cm at Upl Djursholm, Ösbysjön Lake, 11–12, 1941. a—In lake; b—"Warm plot"; c—"Cold Plot". (According to Lindroth, 1943a).

of *Anemone nemorosa* in recent decades in Finland. This was believed to be an indication of climatic improvement and was correlated with enlargement of the areas of a number of birds (Siivonen and Kalela, 1937; Kalela, 1938, p. 239).

It seemed possible to arrive at an idea of *the annual vegetative period* in a similar way, that is, on a phenological basis. Locations with the same length of vegetative period could be joined by isochrones to yield maps that could be compared with those on the mean temperature and the minima of the "critical" months (Figs. 68–71) and with the distribution maps of animals.

I have put in a lot of work to produce such phenological maps for Sweden (according to Arnell, 1923, 1927, 1930). The difficulties are enormous. It is easy to find a suitable phenological manifestation that signals the arrival of *spring*: I chose the first flowering of *Anemone nemorosa*. But a corresponding indication for *autumn* is scarcely to be had, at any rate not from wild-growing plants. The events at this time of year tend to proceed more gradually and are hardly noticeable. By way of experimentation I utilized the leaf fall of *Fraxinus excelsior* and *Populus tremula*. For every observation point I calculated the mean length of the period between the flowering of *Anemone* and the leaf fall of *Fraxinus* and *Populus*, and these figures were mapped.

At any rate the map of "*Anemone–Populus*" showed a certain regularity in the arrangement of figures of the desired vegetative period. Its length in south Skåne is about 180 days, in the Mälar region about 160 days, in Mdp-Ång about 140 days; in the south Swedish highland there is a minimum region with < 160 days. But the gradations are extremely irregular and it was not possible to draw regular, "reliable" isochrones.

Evidently the phenological primary material available to date in Sweden is too erratic for the desired objective. If only series of simultaneous obser-
503 vations of sufficient duration (> 10 years), which would be especially important in view of the climatic changes (pp. 641 ff.), are utilized, the network of stations is so sparse that no isochrones can be constructed. The decision as to which stage of the observed manifestation should be considered is always left to a certain extent to the subjectivity of the observer. So is the question whether he should or should not consider lococlimatically especially favored (or unfavored) localities.

My experience discouraged me from publishing any phenological map on the duration of the annual vegetative period. The available material must be considered inadequate for this purpose.

Kaikko (1940) tried to determine the mean annual vegetative period (the time between the development of leaves and leaf fall) of birch (*Betula*, excluding *nana*) in Finland, and to depict it cartographically by isochrones. The map shows the most favorable figures in the extreme southwest, then in the isthmus of Karelia and in a small region around the southernmost part of Päijänne. Numerous phenological maps of plants and birds in Sweden are

given by Edin (1941), but they are very generalized and cannot be used for the present purposes.

Soil

Animals that are as soil-bound as carabids—with very few exceptions—must be dependent to a great extent on characteristics of the soil. This is especially true of species with burrowing habits even in the adult stage, foremost: *Amara infima*, *Bembidion pallidipenne*, *Broscus cephalotes*, *Clivina fossor*, *Cymindis macularis*, species of *Dyschirius* (at least *D. globosus* and *D. helléni)*, numerous species of *Harpalus* (for example, *H. anxius*, *H. hirtipes*, *H. melancholicus*, *H. neglectus*, *H. rufitarsis*, *H. rufus*, *H. servus*, *H. smaragdinus*, *H. tardus*), and *Omophron limbatum*. The larvae have subterranean habits to a still greater extent. Especially familiar are the tunnels of *Cicindela* larvae.

The characteristics of the ground that are biologically effective—often
504 called *edaphic factors*—are primarily *humidity, physical features* (especially thermal characteristics and particle size) and *chemical features*.

The moisture of the ground is the combined effect of climatic and purely edaphic factors. It was briefly considered above (p. 485). As there emphasized, the ground moisture is primarily an ecologically effective factor, which has a decisive role in the distribution of every species in the landscape (for example Bro Larsen, 1936, pp. 210 ff.) and in their more or less regular movements during the course of the year (see H. Krogerus, 1948, pp. 126 ff.). In an attempt to determine more precisely the ecological character of the "limestone species," and twice in other contexts (pp. 61, 357), various experiments with humidity were carried out. The absence of some xerophiles from western Norway (p. 488) can perhaps be attributed to excessive ground moisture on account of heavy precipitation. Conversely—but also due to the mechanical characteristics of limestone gravel (p. 128)—the xerophiles are obviously favored in parts of southeast Sweden, especially on Öland and Gotland. However, deficient ground moisture cannot completely eliminate a species from any larger region of Fennoscandia. Zoogeographically—with respect to area limitation, evident from the distribution map—the ground moisture in our region is therefore a factor of lower rank and will not be further considered here.

The thermal characteristics of the ground were also considered elsewhere (pp. 177 ff.) in fair detail (see also p. 513).

Hence chiefly two groups of characteristics of the ground remain to be considered here, namely, the importance of particle size and of chemical composition. In Fennoscandia no carabid is associated with outcrop rock (cf. p. 529)—its indirect thermal importance was considered above (p. 186)—and we will therefore focus here exclusively on *loose deposits*.

Size of Soil Particles

The coarser or finer nature of granules determines not only whether an animal can move on the surface but also whether it is capable of burrowing into the ground; it is also secondarily of critical importance for various other characteristics of the ground. Ecologically of greatest importance is the *water-*
505 *holding capacity*, which with decreasing particle size—especially around the size 0.2 mm—enormously increases (Atterberg, 1903; Ekström, 1927, pp. 17 ff.; Stebutt, 1930, pp. 111 ff.). The thermal conductivity also increases thereby. Krogerus (1932, p. 160) concludes that "fine-grained sand provides the organisms with much more favorable ecological conditions than coarse-grained sand," and that "a grain size averaging 0.2 mm represents a limit between the ecologically favorable and unfavorable types of sand."

In the few experiments I carried out in the substratum gradient apparatus with sand of different particle sizes (Experiments 94–103, p. 83) the above secondary characteristics of sand had no role. The samples were kept as uniformly moist as possible, and on account of the short duration of exposure (overnight) the water content could not have appreciably altered during the experiment. Uniform room temperature compensated for any thermal differences between the sand types. The species studied all have a more or less burrowing mode of life. It was therefore intended to investigate whether the purely mechanical characteristics of different types of sand based on particle size, exercise any influence on the carabids (on their burrowing ability). Unfortunately it was not possible to obtain all six kinds of sand from the same native soil (1 and 2, as well as 5 and 6, nevertheless have the same origin), so the mineral characteristics were not exactly the same (1–2 showed traces of limestone, but not the others). Of course the above detailed treatment seems to have revealed that at least the species of *Harpalus* are extremely insensitive to the composition of the soil (pp. 121 ff.). The distribution of the carabids in these experiments gives no reason for assuming that they are influenced by such differences.

The experiments with *Harpalus* (Experiments 97 ff.; Diagram 51) revealed fairly large differences in the response of the species tested. On account of the usual inclination to gather at the ends of the apparatus (p. 73), the diagrams are of course to be utilized only relatively, not absolutely (not as proof of the most preferred sand type). However, it is clear that all species preferred the finer sand types with the exception of *H. serripes*. The diagrams are arranged from this viewpoint. The position of *H. serripes* corresponds to its occurrence in nature. Among the species tested it is the only one that regularly lives on coarse gravel. The sequence of the other species could probably be corrected
507 by using more material. The vacillating behavior of *H. neglectus* (50 specimens) is surprising; the extreme position of *H. rufitarsis* (only 35 specimens) is uncertain. On the other hand the sequence *H. tardus–H. anxius–H. smaragdinus*

goes well with the ecological characteristics of these species.

The two species *Dyschirius obscurus* and *D. thoracicus* were studied in a circular gradient apparatus (Experiments 95–96), and the choice of sand type may thus correspond better with reality (Diagram 52). It is obvious that both species avoid the coarsest sand (2–1 mm). That this is less obvious in *D. obscurus* is undoubtedly due to the fact that this species tolerates the finest sand (< 0.075 mm) better than *thoracicus*, and that in the apparatus the sectors with the finest and the coarsest sand were adjacent. In general, as compared with *D. thoracicus*, *D. obscurus* evinced only slightly the expected stronger attraction to the finer sand types ("mean box" 3.96, as against 3.84 in *D. thoracicus*). Unfortunately the carabid material available was too meager. Both species show a distinct maximum with the particle size 0.125–0.075 mm. Krogerus (1932, p. 164) found that *D. obscurus* in nature prefers sand types < 0.2 mm.

The experiments with *Harpalus* and *Dyschirius* seem to provide the expected result that *the particle size of the substratum has an important influence on the choice of biotope for some carabids, irrespective of secondary differences in*
508 *moisture, temperature, etc.* Ellinor Bro Larsen's contrary findings (1936, pp. 220 ff.) led the author herself to state that in the region investigated (West Jutland) there is insufficient variability of particle size with corresponding moisture.

This state of affairs is actually known to every field entomologist. It is nowhere more evident than along the banks of a large river. Along with usually very smooth transition in the structure of the bank material, from stone and coarse gravel on the rapid upper course through finer and finer sand to the pure loam at the mouth of the river, there is a parallel change in the fauna of the banks. This is true not just of the burrowing forms but also of species that constantly stay on the surface, including numerous carabids.

A few examples of riparian species of fresh water whose dependence on shore material of a particular coarseness (categorization after Atterberg, 1905) seems to be clear, are listed here. The classification is based on estimates, since no measurements of particle size were undertaken in nature.

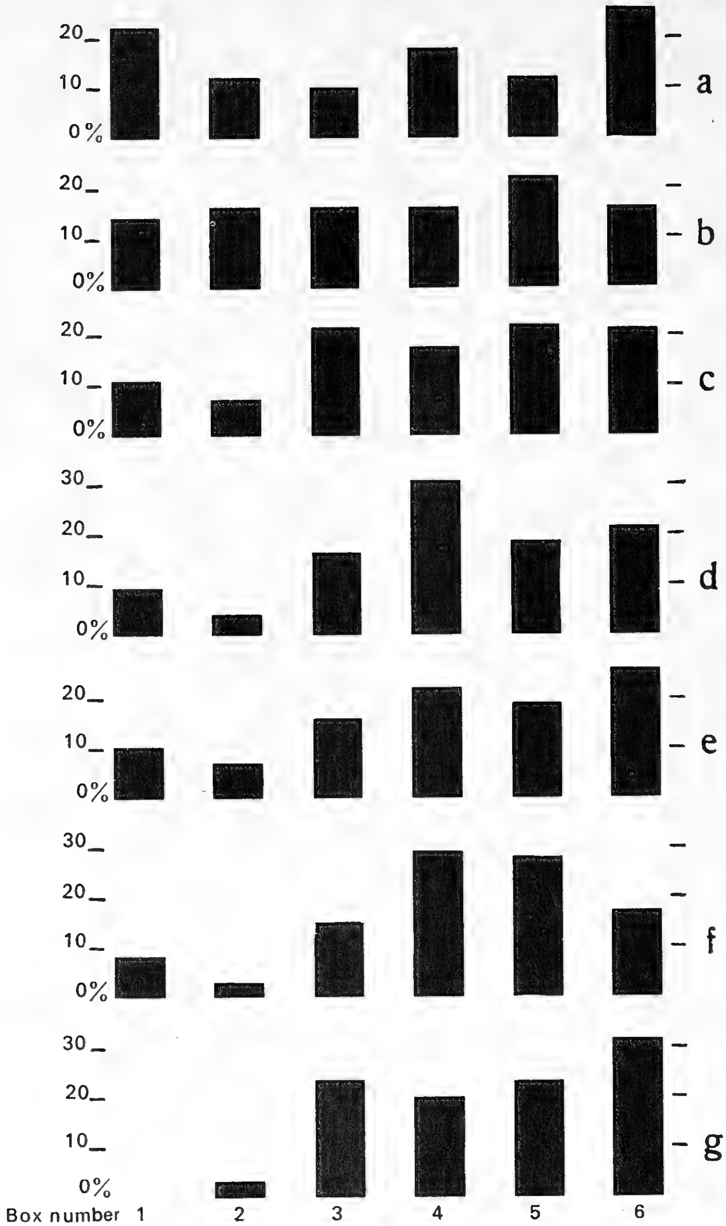
a. In rocky and stony places

Nebria gyllenhali

b. On gravel (pebbles) 20–2 mm in size

(*Bembidion fellmanni*)	*B. saxatile*
(*B. hasti*)	*B. tibiale*
B. hirmocoelum	*B. virens*
(*B. hyperboraeorum*)	(*Perileptus areolatus*).
B. prasinum	

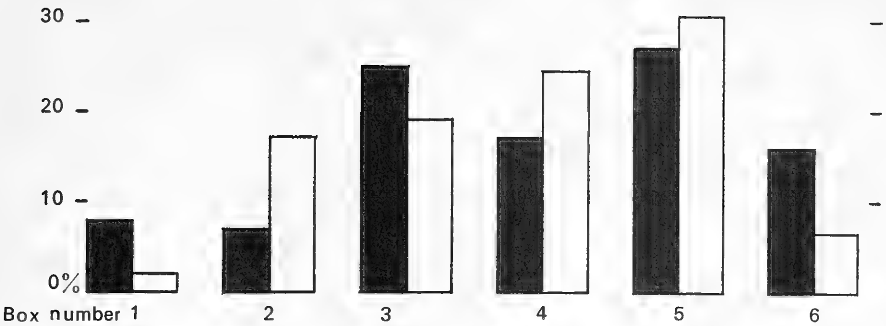
Species in parentheses live more or less regularly on coarse sand.



506 Diagram 51. Distribution of 7 species of *Harpalus* according to different particle sizes of sand in the substratum gradient apparatus.

Types of sand are: 1 = 2–1 mm; 2 = 1–0.5 mm; 3 = 0.5–0.25 mm; 4 = 0.25–0.125 mm; 5 = 0.125–0.075 mm; 6 = < 0.075 mm.

a—*Harpalus serripes*; b—*H. neglectus*; c—*H. hirtipes*; d—*H. tardus*; e—*H. anxius*; f—*H. smaragdinus*; g—*H. rufitarsis*; Experiment 97 ff., p. 84.



507 Diagram 52. Distribution of *Dyschirius obscurus* (black) and *D. thoracicus* (white) according to different particle sizes of sand in the circular gradient apparatus. Experiments 95–96, p. 83. Types of sand as in Fig. 51.

c. On coarse sand, 2–0.6 mm in size

Agonum ruficorne
Bembidion lapponicum
B. velox.

No species is bound to a particular size. *Agonum* seems to require an admixture of loam, and the two species of *Bembidion* also occur on common sand.

d. On "common" sand, 0.6–0.2 mm in size

(*Bembidion andreae polonicum*)
(*B. argenteolum*)
(*B. pallidipenne*)
?*B. repandum*
B. ruficolle
(*Cicindela maritima*)
(*Dyschirius thoracicus*).

509 Almost all species—those in parentheses—also live on fine sand; *Bembidion andreae* likes places with an admixture of loam.

e. On fine sand ("mo"), 0.2–0.02 mm in size

Asaphidion pallipes
Bembidion litorale
B. semipunctatum
B. siebkei
(*B. stephensi*)
Dyschirius angustatus
D. impunctipennis
D. intermedius
D. nitidus
D. obscurus
D. politus
(*Nebria livida*)
(*Omophron limbatum*).

The 3 species in parentheses require—or at any rate prefer—soil with a loam admixture. *Dyschirius obscurus* also lives, in smaller number, in common sand.

f. On silt ("mjäla") and loam, particle size less than 0.02 mm

(Acupalpus dorsalis)
Agonum marginatum
(A. piceum)
Asaphidion flavipes
Bembidion aeneum
B. articulatum
(B. assimile)
(B. dentellum)
(B. femoratum)
(B. guttula)
B. illigeri
(B. lunatum)
(B. lunulatum)
B. nitidulum
(B. properans)
(B. transparens)
(B. ustulatum)
B. varium
(Chlaenius nigricornis)
C. vestitus
(Dyschirius aeneus)
D. lüdersi
(D. septentrionum)
(Pterostichus gracilis)
(Stenolophus mixtus).

Species in parentheses require only a more or less distinct admixture of loam. This may also be true of *Agonum dolens* and *Pelophila borealis*, which are not mentioned. Nonriparian species are considered below.

The zoogeographical—area-limiting—significance of a species that is bound to ground material of a particular particle size naturally depends on how widely the necessary soil type is distributed in the region concerned. Hence two maps are given here (Fig. 77): one on the distribution of *sand and fine sand* (particle size 2–0.02 mm; according to Atterberg's system, 1903, 1905);
512 the other (Fig. 78) on the distribution of silt ("mjäla") and loam (particle size less than 0.02 mm) in Fennoscandia.

Sand (including fine sand)—although often locally limited—shows a fairly uniform distribution in the Fennoscandian region. The large gaps in west and north Norway, and on the Kola Peninsula, are undoubtedly partly due to inaccurate data. Regions especially poor in sand are found in East Småland, in the Mälar Lake region, and in west-central Finland. In the north, the sand is largely limited to the middle and lower reaches of the larger rivers.

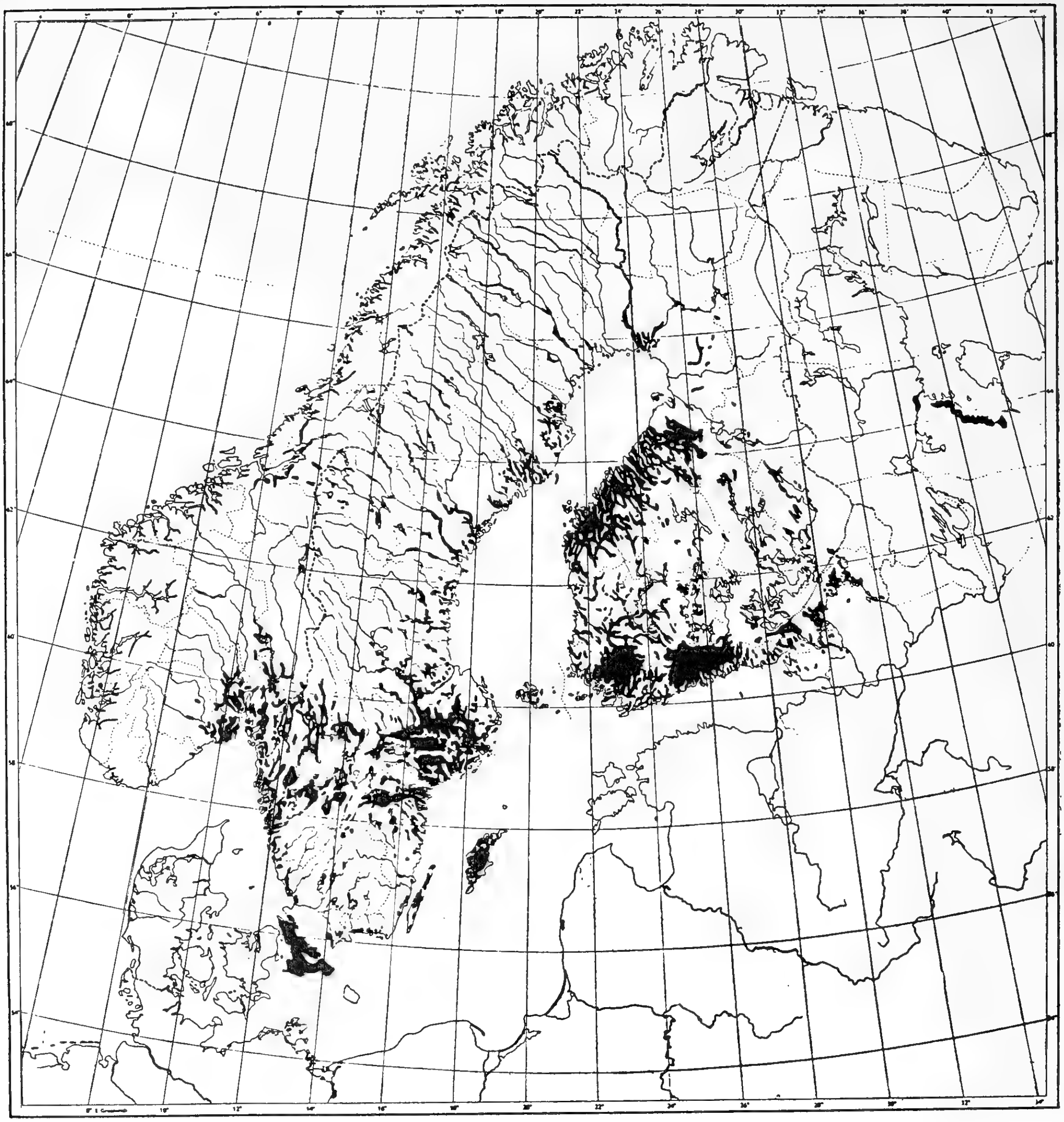
It is scarcely possible to cite a species whose dependence on sand is reflected in an area corresponding in every detail with the occurrence of sand on the map (Fig. 77). Because of its small scale the map is too generalized, and very small isolated sandy places are not marked at all. *Dyschirius politus* seems to be the best example of a correspondence, at any rate in principle. In addition to its absence from west Norway this species shows gaps in the above-cited three regions in Sweden and Finland.

Roughly the same gaps in distribution are evident in the following species, which are more or less closely bound to sand:

a. Missing from west Norway

Asaphidion pallipes
Bembidion litorale
B. semipunctatum
B. velox
Cicindela maritima.

510 Fig. 77. Distribution of sand and fine sand ("mo") in Fennoscandia. From Atlas öfver Finland (1910), Thunmark (1937), Lundqvist (1942), Sahlström (1944–48), and unpublished data of Lundqvist. Conditions in Norway and in Russian parts are broadly generalized.



511 Fig. 78. Distribution of silt ("mjäla") and loam (including moraine clay) in Fennoscandia. Sources as in Fig. 77.

It is nevertheless difficult to decide whether this absence in the west is edaphically determined. For *Amara fulva*, mentioned above (p. 488), which shows a striking predilection for sand—but is not completely dependent on it—*climatic factors* are believed responsible for its western limit. Insufficient summer heat, excessive humidity and lack of sunshine can be as effective area-limiting factors for true sand-dwelling animals as lack of sand (probably more correctly: the rare occurrence of sand) in west Norway. The above 5 species are distinctly heat-requiring (for *Cicindela* see Krogerus, 1932, p. 146; 1937, p. 299) and heliophilous (less distinctly *Asaphidion*).

b. Missing from East Småland

Asaphidion pallipes	*Nebria livida*
Bembidion litorale	*Omophron limbatum.*
B. velox	

513 Especially for *Omophron* the restriction to western Småland is very striking. It is scarcely possible to explain this characteristic in any other way than by the rarity of suitable biotopes in the east.

c. Missing or sparse in central Swedish loamy region (especially around Mälar Lake)

Asaphidion pallipes	*Pterostichus lepidus.*
Cicindela silvatica	

The isolated records of the two last-mentioned species in the region in question were all made, significantly, on sandy diluvial gravel ridges ("rullstensåsar"), which show up on the "sand map" as narrow bands.

d. Missing from west-central Sweden

Bembidion nigricorne	*Cicindela maritima*
? *B. ruficolle*	*Dyschirius obscurus.*

However, in all these four cases it is fairly evident that factors of immigration history have also been effective in the Finnish distribution (see pp. 718 ff.). The above-mentioned big gap is not due just to existence factors. But any region where the biotopes suitable for a species are sparsely situated has an obstructive influence by slowing down the dispersal process.

Bembidion nigricorne rates special interest because this species occurs as an exclusively sand-dwelling animal only in northern Europe (probably also in the British Isles). In central Europe it also lives on more or less moist bog soil, i.e. in the company of *B. humerale*. It is difficult to explain this behavior in any other way than that in cooler regions the carabid looks for as warm habitable biotopes as possible, which is proof of the thermally favorable characteristics of sand. Its thermal conductivity is much greater than that of bog soil (Geiger, 1942, p. 30), so the temperature in the sun must be higher. Even sand-loving *Bradycellus harpalinus* is less choosy in central Europe. It

has already been shown that southern insects in central Europe may become stenotopic sand-dwelling animals near their northern limit (Kühnelt, 1934, p. 122).

In the same way the peculiar "double" occurrence of *Demetrias monostigma* and *Dromius longiceps* is perhaps microclimatically determined, and to a lesser extent that of *D. sigma*. Especially in the case of *Dromius longiceps*, it is evident that the predilection for sand increases in northern Europe. Likewise, *Dromius melanocephalus* and *D. nigriventris* are less distinctly xerophilous
514 ("psammophilous") in central Europe. Concerning the association of the arboricolous species *Dromius angustus* with sand, see below (p. 543).

Loam (clay, including silt = mjäla) in Fennoscandia has a far more characteristic occurrence than sand (Fig. 78). It is concentrated in regions covered by the sea (and the Ancylus Sea) during the postglacial period. In addition, in south Sweden—especially in the southwestern half of Skåne—there is "claymarl" (moraine clay). Otherwise, above the highest shoreline there are only very small, isolated loamy areas.

It should therefore be easier to establish a correspondence between the "loam map" and the Fennoscandian distribution of one or other "loam species," and to deduce a causal connection. This applies especially to the following species (less evident for those in parentheses):

(*Acupalpus meridianus*)
Agonum marginatum
(*Amara famelica*)
Bembidion articulatum
B. assimile
B. illigeri
(*B. varium*)
(*Dyschirius aeneus*)
D. lüdersi.

In Sweden the avoidance of the south Swedish upland on the western side is especially characteristic for these species. One should remember that these clay-deficient regions of south Sweden are also climatically very unfavorable, chiefly thermally (pp. 463, 474 above). But the area of *Bembidion articulatum* or *B. varium*, but especially of *Dyschirius lüdersi*, in Finland extending far northward shows that at least in the case of these species, absence from the south Swedish upland can scarcely be due to climate. On the contrary, these represent examples of species whose Scandinavian area has developed primarily due to edaphic factors.

In Skåne, where the southwestern and northeastern halves of the province are counterparts for the distribution of loam and sand respectively, the influence of the two kinds of soil can be studied in greater detail. Loam-dwelling species are occasionally restricted to the southwestern, loamy half:

Bembidion assimile
B. obtusum
B. properans
Chlaenius vestitus.

515 A larger number of species—not necessarily bound to loam, but not found on pure sand—are missing (as far as is known) at least along the sandy east coast of the province:

Anisodactylus binotatus	*Cicindela campestris*
Asaphidion flavipes	*Dichirotrichus pubescens*
Bembidion aeneum	*Dyschirius salinus*
B. minimum	*Trechus rubens.*

This is partly true even of species that are otherwise abundant almost everywhere and are more or less ecologically distinct ubiquists:

Amara ingenua	*Pterostichus oblongopunctatus*
Bembidion gilvipes	*P. vernalis.*

Even *Carabus granulatus* and *C. violaceus* as well as *Pterostichus coerulescens* and *P. cupreus*, are poorly represented in eastern Skåne. Although these regions have not been thoroughly explored for a long time it is difficult to explain these features otherwise than by the edaphic conditions.

Loam exerts an indirect influence, since lakes in loamy ground become more or less markedly *eutrophic* (s. lat.) (compare the map on the lake districts of south Sweden in Naumann, 1932, p. 45, with the "loam map" above, Fig. 78, p. 511). Several carabids are bound to the shores of such lakes. However, it may not be the loam that is effective (at any rate not the particle size) so much as the thermal or chemical characteristics of the water and of the shore material. The question is partly considered below (p. 528).

In loose mineral deposits of nonfluvial nature—primarily in moraine—particles of the most diverse sizes are usually randomly mixed, and any correlation of the animals living there with definite sizes of particles is dubious. One reason is the often low requirements of the animals for material of definite particle size. Especially in more or less pronounced xerophiles, it also happens—even if the soil consists of fairly uniform sized particles—that they may tolerate very diverse particle sizes, if only the humidity is suitable.

As examples of such more or less eurytopic xerophiles the following species may be mentioned:

	Amara aenea	*Calathus erratus*
516	*A. bifrons*	*Cicindela hybrida*
	A. consularis	*Harpalus fuliginosus*
	A. equestris	*H. melancholicus*
	A. infima	*H. tardus*
	A. praetermissa	*Masoreus wetterhalli*
	A. quenseli f. typ.	*Notiophilus pusillus*
	A. tibialis	*Olisthopus rotundatus*
	Broscus cephalotes	*Pterostichus lepidus.*

Chemical Properties of the Soil

In the section on "limestone species" (pp. 121 ff.) no purely chemical effect of limestone rock on the species studied (chiefly those belonging to the genus *Harpalus*) was established. However, this does not justify saying that the carabids are generally insensitive to the chemical composition of their substratum.

Special attention has been drawn to the apparent dependence of some insects on *common salt* (NaCl). A distinction has been drawn between *halobiont* (salt-requiring) and *halophilous* (salt-loving) animals (Schaum, 1843, p. 180; Benick, 1926, p. 65; Lengerken, 1929a, b).

The source of salt is the sea. Irrespective of this, the conclusive evidence of a species being halobiont is not that it occurs only on the seashore but that inland it is restricted to isolated *saline places*. It must be experimentally investigated whether *Aëpus marinus*, which throughout its area never occurs away from the seashore, really owes its habits to NaCl. On the other hand the halobiont nature of *Dichirotrichus pubescens* is evident from the distribution alone.

In Fennoscandia there are no inland places with NaCl (on the other hand there are "alaun soils" with SO_3, CaO, Al_2O_3, etc.; Aarnio, 1922). Hence in our region halobiont species must live *exclusively*, and halophiles at least *predominantly*, on the seashore.

There are only 5 quite unambiguous halobionts in our region (in central Europe they also inhabit inland saline places):

Anisodactylus poeciloides
Dichirotrichus pubescens
Dyschirius chalceus
D. salinus
Pogonus luridipennis.

In addition there are *Aëpus marinus* and *Trechus fulvus* which are bound to the seashore throughout their area (however, there are different subspecies
517 of *Trechus* living in caves in the Iberian Peninsula), but their dependence on NaCl is not proven. *Amara convexiuscula* (see below) is doubtful.

The following species might be suspected of being *halophiles*:

Bembidion aeneum
B. fumigatum
B. minimum
B. pallidipenne
Dyschirius impunctipennis
D. obscurus.

Doubtful cases are *Agonum archangelicum*, *Bembidion chaudoiri*, and *B. repandum*, which occur within the region only on the shores of the White Sea. Their distribution and ecology are not fully known. Sufficient information has been provided in Part I of this work on further species which have been unjustifiably considered as halophilous or halobiont.

To judge the salt requirement of the species in question a map of the salinity of the surface of the Baltic Sea in the Kattegatt and Skagerrak (Fig. 79)

may serve as the starting point. According to their tolerance of slightly saline water the above 5 halobionts can be arranged in the following order by their saline requirement:

1. *Pogonus luridipennis*. Also in Germany (aside from inland records) only on the North Sea coast; the old records from the Baltic Sea coast are doubtful (Horion, 1941, p. 186).

2. *Dyschirius chalceus*. In Sweden—like the following species—as far as the southwestern edge of Skåne. But the species is missing from the southern Danish islands, and is recorded from the German Baltic Sea coast only by a single specimen near Travemünde (Horion, 1941, p. 99).

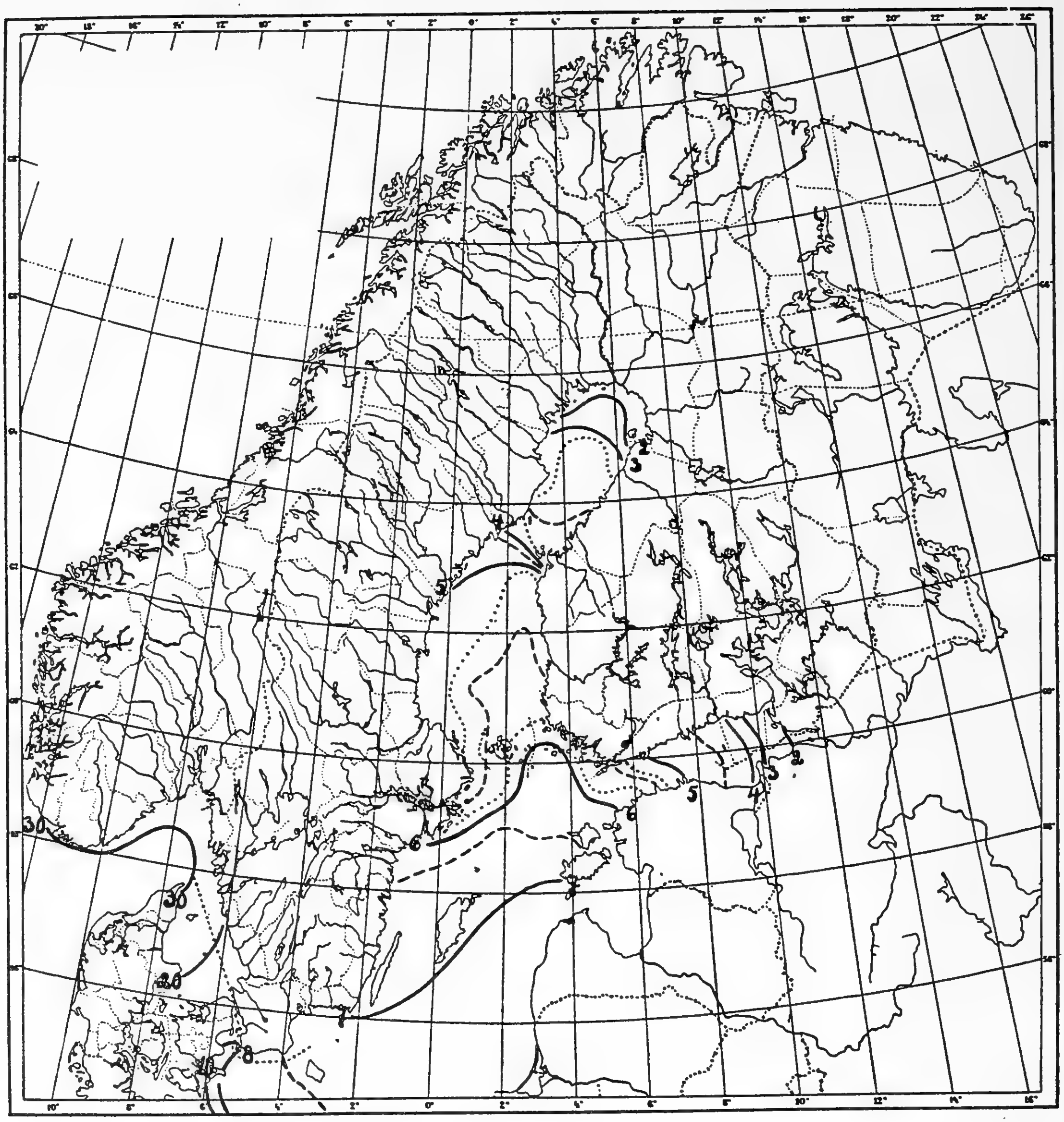
3. *Anisodactylus poeciloides*. Also in Lolland and Falster as well as on the German Baltic Sea coast, eastward at least as far as Warnemünde (Horion, 1941, p. 250).

4. *Dichirotrichus pubescens*. The record in Ögl may be accidental (transported with ballast ?), but the more or less continuous distribution extends at least to central Gotland. The gap in eastern Skåne and Blekinge is fully explicable by the absence of loam. Along the German Baltic Sea coast as far as East Prussia (Horion, 1941, p. 244). In the White Sea the saline content still in Onega Bay is more than 20‰ (Knipovitsch, 1906, pp. 1171–1174) and its occurrence there is thus quite natural.

5. *Dyschirius salinus*. The only species of the five halobionts that reaches the Finnish Baltic Sea coast. In Sweden it is unknown north of Små Kalmar and Gotland. This area limit, so unevenly situated on opposite sides of the
519 Baltic Sea, is explained by the course of the isohalines (Fig. 79). *Bembidion minimum* (see below) is of the same distribution type. A very good correspondence between the course of the isohalines and the distribution of *Crambe maritima* in the same regions of Finland was found by Eklund (1931, pp. 101, 125).

Amara convexiuscula has been designated halophilous by all the authors cited above (with the exception of Schaum, 1843; also by Håk. Lindberg, 1931, pp. 148, 164). Inland in central Europe it does not occur only at saline places but also "on scree-slopes close to cities." Horion (1941, p. 271) assumes that "these ground locations show a certain salt content." It is quite possible that this species is dependent on substances other than the NaCl present in seawater, but this can be decided only experimentally. Backlund (1945, pp. 108 ff.) has shown that some animal species of seaweed banks in preferendum experiments respond positively to iodides and nitrates, but this has not so far been established for insects.

The 6 suspected "*halophiles*" mentioned above form a very heterogeneous group. They share the feature that they live chiefly (*Bembidion fumigatum* exclusively in our region) along the seashore, but there are records from the shores—as far as can be judged—of bodies of fresh water (of the cited *Bembidion* in Denmark and central Europe).



518 Fig. 79. Mean surface salinity of the Baltic Sea, in $^{0}/_{00}$. Isohalines of one-half per mille are broken, those of one-fourth per mille dotted.

From Atlas öfver Finland (1910), and Deutsche Seewarte (1927).

Bembidion pallidipenne, *Dyschirius impunctipennis*, and *D. obscurus* occupy a special position in that their occurrence on fresh-water bodies is rare, yet so regular that there can be no question of chance (however, *D. impunctipennis* occurs in our region constantly only on Lake Ladoga; also in Germany, Horion, 1941, p. 99 and Latvia). It must be concluded that for these 3 species what is decisive is not the NaCl content of the soil but the presence of suitable sandy soil of a definite particle size, and possibly also definite hygric and thermal characteristics, chiefly on the seashore. For the species of *Dyschirius* an important role is played by the frequent mass occurrence of its normal prey, *Bledius arenarius* Payk., where it lives. Both Håk. Lindberg (1931, pp. 154, 164) and Krogerus (1932, pp. 171, 173) believe that the two species of *Dyschirius* are not bound to NaCl. *Bembidion pallidipenne* occupies the same position. Hence in these cases there is no reason to speak of "halophily," since this word means the species "loves" common salt (NaCl), not the sea.

520 The three remaining "halophiles," all belonging to the genus *Bembidion*, behave differently. *B. minimum* in our region almost always inhabits the seashore (on loam). The only freshwater record, which was not purely accidental, is from Öland, where the species to some extent corresponds to *B. aeneum*, considered below. It is noteworthy that the northern limit in the Baltic Sea region in principle corresponds with that of the halobiont *Dyschirius salinus*, which often supersedes it, such that, following the isohalines, in Finland it extends much farther north than in Sweden. Much the same can be said of the halobiont aquatic plant *Ruppia spiralis* (Samuelsson, 1934, p. 16). The difference between the two carabids is that *Bembidion minimum* has everywhere advanced farther—at the Swedish east coast, in Finland both at the west coast and at the Gulf of Finland. The records along fresh water in central Europe are "very sporadic and rare" (Horion, 1941, p. 156); significantly, the species was once found "at a salt-lick for sheep." We may conclude from this that *B. minimum* is not indifferent to NaCl.

It is probable that *Bembidion fumigatum* behaves like *B. mininum* in its response to NaCl. However, the species is very rare in our region and the records from other regions are not precise enough to go beyond conjecture.

It might be worthwhile, however, to study the distribution of *B. aeneum* more closely (considered on p. 399 from the dynamic viewpoint). At first sight the distribution of this species in its Fennoscandian area does not suggest "halophily." There is continuous distribution along the west coast but there is also a broad, slanting belt across central Sweden; inland records are also known from southeastern Norway and from Öland. *B. aeneum* might thus be presumed to be a loam-dwelling species, and it is in fact bound to loamy soil. But—with the exception of the record of a single specimen near Uppsala—why is it missing from the Mälar Lake region? This cannot be a dynamic (temporally determined) limit, since southeastern Dlr was reached.

The work of S. Johansson (1926, p. 21) led me to venture an explanation. He studied the chlorides in the tapwater of the city of Skara in Vgl and
521 established that the striking amount thereof is due to the presence of NaCl in the loamy soil (found at least at a depth of 1.5–9.5 m; samples from the top layer were not studied). Since Yoldia loam is present here, Johansson surmised that the common salt originated from the seawater in which the loam formed a deposit.

The map on the distribution of Yoldia loam (Fig. 80) shows an inter-
522 esting correspondence with the inland distribution of *Bembidion aeneum* in Scandinavia. This species differs from other loam-dwelling species, such as *B. articulatum*, *B. illigeri*, etc. (p. 509) primarily by its almost complete absence from the eastern part of the central Swedish loam region (cf. loam-map, Fig. 78, p. 511), *in regions that were submerged even during the Ancylus period*, that is, where the saline Yoldia loam was covered with freshwater deposits.* A broadly corresponding distribution in Sweden is shown by *Elatine hexandra* (Samuelsson, 1934, p. 85). It would be worthwhile investigating whether a certain amount of NaCl in the water bodies has a positive role for this plant too.

The following details of the map (Fig. 80) are especially striking:

1. In Skåne: All 5 records lie below the highest marine boundary, even though extensive loam regions (moraine clay) are also present above it (Fig. 78).

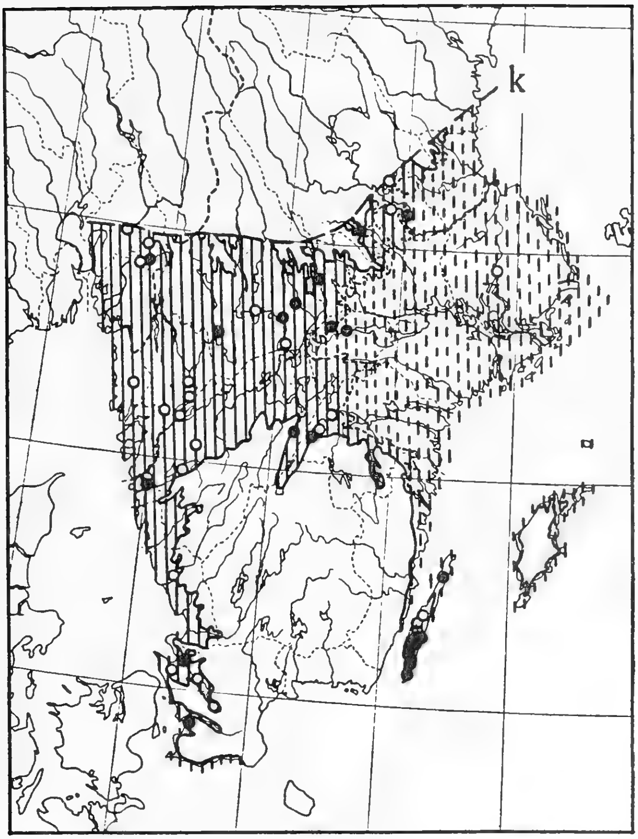
2. In central Sweden: There is one single record (Upl Uppsala, 1 specimen)—possibly of an accidental nature—from the middle of the "Ancylus region." Constant populations exist partly in the "Yoldia region" and partly on the western limits of the "Ancylus region" (Nke Örebro; Dlr Ludvika and Hedemora), where the freshwater deposits must be sparse.

3. The northernmost inland records of *Bembidion aeneum* (in southeastern Norway, in Vst and Dlr) are immediately south of the so-called K-line, which according to Munthe (1940, pp. 79–83) represents the southern limit of inland ice at the end of the Yoldia period. But this line does not signify the limit of loam (see map, Fig. 78), so is not an existence limit for *B. aeneum*.

Given these facts, it seems to be justified to assume that *B. aeneum requires a very low NaCl content in the substratum*. The only records in the region that contradict this are from the alvar areas of Öland, the southern two-thirds of which was submerged in the postglacial period only during the time of the Baltic ice sheet, thus during a freshwater period.

The effect of NaCl on an animal species should of course also be studied experimentally, most simply by preferenda experiments. Such studies have been carried out by Ellinor Bro Larsen (1936, p. 200) and Backlund (1945, p. 105).
523 The first found a distinctly positive response to NaCl in two species of *Bledius* from the seashore.

*The latter Littorina deposits seem to play no positive role for *Bembidion aeneum*.



521 Fig. 80. *Bembidion aeneum.* Scandinavian inland records. Blank circles—one specimen only. Regions submerged by Yoldia Sea (south of ice edge, k, of that time) are vertically hatched. Broken lines: parts later covered by Ancylus Lake. Geological limits taken from Munthe (1940).

It was especially interesting to study *Bembidion aeneum* experimentally. Unfortunately little material of living carabids was available to me, but the experiments were repeated until 50 observations were complete. *B. minimum* was selected as the species for comparison, for which—as mentioned above—dependence on NaCl was to be expected. The material of both species originated from the seashore near Boh Sämstad.

To find a suitable saline content for the following alternating experiments, first of all *B. minimum* alone was studied in a serial experiment with NaCl of

different concentrations (Experiment 93a, p. 82). Result:

	Spring water	1/8%	1/4%	1/2%	1%	2%	NaCl	Total
No. of specimens	1	3	0	3	8	4		19

In the alternating experiments I used cuvettes containing sand, moistened alternately with spring water and 1% NaCl (Experiments 92a, 93b, p. 82). Both species were tested together:

Material from Boh Sämstad	Spring water	1% NaCl	Total
		Specimens	
Bembidion aeneum	16	34	50
B. minimum	17	33	50

Bembidion aeneum apparently shows the same attraction to NaCl as *B. minimum*. One source of error was that the material originated from a saline locality (the seashore). It is conceivable that this population would behave in a different way to NaCl than carabids from the inland, either on account of genetically determined "race characteristics" or due to alternative adaptation. The material comprised brachypterous as well as macropterous individuals, whereas in the inland only the macropterous form occurs (see map, Fig. 49, p. 400).

Hence it was important to study macropterous inland specimens too, and with difficulty I obtained a small number of *B. aeneum* from Öld Möckelmossen. The experiments (Experiment 92b, p. 82) gave the following results:

Material from Öld Möckelmossen	Spring water	1% NaCl	Total
		Specimens	
Bembidion aeneum	9	41	50

Hence the macropterous inland form of *B. aeneum* shows at least as strongly positive a response to NaCl as the dimorphic coastal form or as
524 *B. minimum*. This experimental result therefore confirms the "cartographic" concept that the Scandinavian inland distribution of *B. aeneum* is dependent on Yoldia loam.

The unexplained exception is the occurrence on the Alvar region of Öland, which in the postglacial period—according to geologists—was underwater only in the time of the Baltic ice sheet (a freshwater period). I cannot decide whether physiologically NaCl can be replaced by $CaCO_3$ (however, *B. minimum* was also found in Öld at a "nonsaline" site); a similar occurrence is shown by the hydrophilid *Ochthebius marinus* Payk. (Håk. Lindberg, 1948,

p. 159). If the effect of NaCl on the animals is mainly of osmotic nature, this would be possible. Analysis of a loam sample from the locality Möckelmossen, however, revealed a slight Cl content (1 per mille). The actual physiological significance of NaCl for halobionts can be determined only on the basis of careful experiments.

At any rate it seems to me improbable that there would be animals that "love" NaCl without requiring a certain minimum quantity of it. Future detailed explorations will doubtless show that the heterogeneous group of the "halophiles" is divisible into two sections:

1. Halobionts, requiring NaCl, which are satisfied with such small quantities that they can live away from the seashore at virtually nonsaline sites. Examples: *Bembidion minimum*, *B. aeneum*, probably *B. fumigatum*, possibly *Amara convexiuscula*.

2. Species indifferent to salt, which find conditions suitable for life on the seashore for other reasons (possibly also at other saline sites). Examples are animals of *sandy ground* ("psammophilous" species) such as *Dyschirius obscurus*, *D. impunctipennis*, *Bembidion pallidipenne*, and *Cicindela maritima*. Other animals may be associated with halobiont plants or animals for *food habit requirements* (examples have been provided by Krogerus, 1932, pp. 173–174). At the area limits, the *microclimatic* effect of the sea also has a role. The occurrence of *Bembidion saxatile* in central Europe, and of *Nebria gyllenhali* on Gotland, can be explained in this way. Finally, it is conceivable that salinity-tolerant animals on the seashore, as has long been assumed of the "halophytes" among the plants, enjoy the reduced *competition,* and that at localities with
525 saline content they are free from some other natural *enemies* (animals, fungi, bacteria) (examples have been provided by Ellinor Bro Larsen, 1936, p. 207).

Evidently salts and chemical compounds other than NaCl may also exercise a positive effect on carabids. Of course it may be pointed out that more detailed analysis of the importance of $CaCO_3$, (pp. 120 ff.) failed to reveal any unambiguous chemical effect on the insects. Concerning the importance of the "nutrient salt content" of the ground—at any rate with regard to the Fennoscandian carabids—I have come to a different conclusion than Holdhaus (1911a, 1911b).

In a different context I had the opportunity to carry out a series of experiments which also touched on this complex of problems. A number of clearly *synanthropous* species have greatly extended their area (see p. 637) during the last decades—chiefly northward—and we cannot attribute it just to enhanced possibilities of passive dispersal. For one of these species, *Amara fusca*, it was assumed in central Europe that "the more abundant occurrence of this species is associated with the increasing use of certain synthetic fertilizers" (Nürnberg in Horion, 1941, p. 261). Since I surmised that similar factors would apply to the definite area displacement of *Amara ingenua* (p. 630) (Part I, p. 140) I decided to investigate the problem experimentally.

Amara ingenua was studied in the substratum gradient apparatus with the usual synthetic fertilizers, at first in serial experiments, where a suitable concentration of the substance was tried out for the alternating experiments that followed. As control species—used only in the alternating experiments—*A. praetermissa* was selected, which is shy of cultivation and seems in no way to be favored by it.

The experiments here have been arranged according to the substances tested (pp. 80 ff.; cf. also Experiment 107 and p. 74).

1. $Ca(NO_3)_2$. Serial experiment (Experiment 84a).

	Distilled water	1/4%	1/2%	1%	2%	3%
Amara ingenua	23	12	6	3	8	5
	4%	5%	7 1/2%	10% salt	Total	
	6	8	15	14	100 specimens	

$Ca(NO_3)_2$. Alternating experiment (Experiments 84b, 89).

	Distilled water	5% $Ca(NO_3)_2$	Total
Amara ingenua	34	32	66
A. praetermissa	66	34	100

526 2. Phosphates.

a. Thomas phosphate (commercial product). Serial experiment (Experiment 85).

	Distilled water	0.075%	0.15%	0.3%	0.6%	
Amara ingenua	9	6	6	9	3	
	1 1/4%	2 1/2%	5%	7 1/2%	10% salt	Total
	0	1	2	1	7	44 specimens

Thomas phosphate is hard to dissolve and correct gradation of low concentrations was too uncertain, so superphosphate was used.

b. Superphosphate. Serial experiment (Experiment 86a).

	Distilled water	1/4%	1/2%	1%	2%	
Amara ingenua	11	10	7	6	8	
	3%	4%	5%	71/2%	10% salt	Total
	5	6	8	6	5	72 specimens

Superphosphate. Alternating experiments (Experiments 86b, 90).

	Distilled water	2% superphosphate	Total
		Specimens	
Amara ingenua	36	36	72
A. praetermissa	48	52	100

3. KCl. Serial experiment (Experiment 87a).

	Distilled water	1/4%	1/2%	1%	2%	3%
Amara ingenua	6	12	14	14	6	8
		4%	5%	7 1/2%	10% salt	Total
		9	6	5	3	83 specimens

KCl. Alternating experiments (Experiments 87b, 91).

	Distilled water	1% KCl	Total
		Specimens	
Amara ingenua	56	43	109
A. praetermissa	56	44	100

4. Liquid ammonia (commercial product). Two alternating experiments (Experiments 88a, b).

	Distilled water	Distilled water	Distilled water	
Amara ingenua	7	7	1	
	1%	2%	3% liquid ammonia	Total
	0	1	1	17 specimens

	Distilled water	Distilled water	Distilled water	
Amara ingenua	7	4	2	
	1/8%	1/4%	1/2% liquid ammonia	Total
	0	0	2	15 specimens

Since the species showed such a strong aversion to liquid ammonia no comparative experiment with *A. praetermissa* was required.

The experiments show that *Amara ingenua* does not respond positively to any of the usual synthetic fertilizers, not even ammonia. The only difference that could be surmised from *A. praetermissa*, which is not favored by cultivation, is that *A. ingenua* tolerates the superphosphate better (but without responding positively to it).

It seems to be justified to conclude that *A. ingenua* is not chemically favored by modern synthetic fertilizers, at least not directly, and that its recent

area expansion cannot be explained on this basis. On the other hand the species shows a distinct predilection for certain synanthropous plants with respect to
527 its food habits, which is dealt with below (p. 539). To the extent that these plants are dependent on fertilizers we can of course speak of the *indirect* effect of these substances on the insect.

Another chemical factor of the soil to which a very important role has been ascribed, at least for the growth of plants, is the soil reaction, which means the hydrogen ion concentration expressed as the pH. How far this factor is crucial for the ground fauna too is a problem that has been taken up for more detailed study by Krogerus in his extensive work on bog fauna, yet to be concluded. In a preliminary communication (Krogerus, 1939, pp. 1222 ff.) he mentions a number of bog species that are "stenoionic," i.e. they tolerate only a slight variation in the soil pH. He also mentions 3 carabids, *Agonum ericeti*, *Dyschirius helléni*, and *Elaphrus lapponicus*, the first of which was also experimentally studied, where it was found to give a very strong positive response to the acidic substratum. In a personal communication he added *Agonum munsteri* (somewhat less pronounced) (on the other hand *A. consimile* is "acidophobic"). The above species rank among the most stenotopic of all Fennoscandia carabids, since they inhabit only bog soil of a particular type. It would be interesting to investigate *Bembidion humerale* experimentally for this character.

My own investigations in this field are restricted chiefly to an experimental study of some more or less xerophilous "limestone species," which could be expected to respond positively to *alkaline* soil conditions. This did not prove to be the case (pp. 122 ff.). The insects were found to be totally indifferent to the soil pH, and I have suggested reasons (p. 125) why xerophilous animals might be expected to be so.

The observations on the occurrence of *Brachynus crepitans* and *Agonum dorsale* in nature confirm my view. At several localities where these species occur together, I electrometrically determined the pH and found a variation from 4.5 (Ögl Mogata) to 7.9 (Öld Greby).

Even strongly hygrophilous species can show indifference to pH: *Pterostichus anthracinus* lives in Upl Djursholm with a pH of 4.8, and at a locality in Öland (Halltorp) with a pH of 6.3. Individuals that were reared from the egg onward at a pH of 4.8 even showed a slight preferendum for a pH of 7.5 in the substratum gradient apparatus (Experiment 46, pp. 77, 356).

528 Krogerus' experimental observations (in litt.) also show that most of the hygrophilous carabids are indifferent to pH. Interestingly, he found that a few species are more or less markedly *neutrophilic or alkaliphilic*. He mentions *Agonum thoreyi*, *Badister peltatus*, *Chlaenius tristis*, and *Pterostichus aterrimus*.

These species are typical members of the shore fauna of eutrophic bodies of water. It would be interesting to study the remaining ecologically corresponding species experimentally for the pH factor, chiefly:

Agonum lugens	*Bembidion transparens*
A. moestum	*Odacantha melanura*
Badister dilatatus	*Pterostichus gracilis.*

With regard to *Oodes gracilis* I have proved that thermic factors are decisive (Lindroth, 1943a), and the same may hold true for the almost identically distributed *Demetrias imperialis.*

In conclusion, concerning the area limiting significance of the soil reaction, it may be stated that a clear response to the pH is to be expected only in hygrophilous species, and that even among these only a few species will turn out to be "stenoionic." But even in such cases it must be ascertained whether the hydrogen ion concentration actually represents the decisive *factor*, or is more an *indicator* of other characteristics of water, essential for the life of the animals (p. 196). I am not aware of the reasons for Dahl's view (1928) that various carabids love "humic acids."

Subjectively, I would be more inclined to accept the soil pH of acidic bogs as a "factor" than the response of species to eutrophic (s.l.) lakes, since these bodies of water are also purely chemically characterized by many other peculiarities (see Naumann, 1932, p. 114; Thunmark, 1937, p. 19).

A chemical effect of the substratum is also conceivable for the few species that are ecologically more or less closely associated with burned wood. Foremost among these are *Agonum bogemanni* and *A. quadripunctatum*, which live chiefly under the bark of trees damaged by fire, and *Pterostichus angustatus*, which—although an exclusively ground insect—tends to appear at places lately
529 devastated by forest fires. Without experiments it is not possible to determine the factor responsible for this choice of biotope by the carabids. Here I merely draw attention to the information provided for the species in Part I of this work (and in the Supplement herewith).

There are other examples of insects with a strong positive response to the smoke of burning. Linsley (1943a, p. 342), in his observation on the genus *Melanophila*, writes: "In summary, the buprestid beetles of the subgenus *Melanophila* s. str. appear to be attracted over long distances by smoke from a variety of burning materials, including wood, oil, mill refuse, smelter products and possibly tobacco. In nature this attraction leads them to forest fires where they normally oviposit in scorched coniferous wood."† Swedish foresters are familiar with the fact that the capricorn beetle, *Monochamus sutor* L., often comes flying in swarms while a forest fire is raging.

In this section a few words remain to be said on the term *petrophily* proposed by Holdhaus (1911a, 1911b, 1927–28). He labels petrophilous "such species as live only on bedrock, i.e. on substrata arising from bedrock. Petrophilous species avoid all loose rocks and are therefore missing from deep sand and rubble deep loamy sediments, and with few exceptions from loess and

†(Original citation in English; suppl. scient. edit.).

tegel subsoil" (1911a, p. 728; 1911b, p. 323). * The phenomenon of petrophily is explained by Holdhaus mainly by the strongly fluctuating *nutrient content* of the ground: "Both, the chemical and the physical characteristics of the ground or of water exercise an influence on the fauna. However, it appears that greater importance is to be ascribed to the chemical factors" (1911a, p. 742; 1911b, p. 342). Among the physical characteristics he considers chiefly the water-holding capacity, but attaches practically no importance to thermal factors.

In Fennoscandia, petrophilous animals would be expected in the *fjelds* and on outcropping *Cambro-Silurian limestone*—especially on Öland and Gotland. Among the "limestone species" of the south, to which a separate section
530 was devoted, it might be possible to designate a small number of carabids as "petrophilous" to the extent that they are apparently favored by outcropping limestone rock, for example, *Harpalus azureus*, *H. rupicola*, *H. serripes*, *H. vernalis*, perhaps also *Cymindis humeralis*. But it was evident as well, that in these cases it is the *physical*—chiefly *thermal*—characteristics that are primarily favorable.

In the fjelds only one species, *Nebria nivalis*, comes to mind. It is the only Fennoscandian carabid clearly and exclusively resident in the *Regio alpina*, where it lives at the edge of perennial snow drifts, chiefly on firm rock or thin moraine. However, the occurrence of this species, in the Abisko region as elsewhere, shows that it makes no distinction between sedimentary limestone rock, chiefly along the western part of Torneträsk (see map, Fig. 9, p. 113) and limestone-deficient eruptive rock, and generally between different kinds of rock. *Nebria nivalis* cannot be considered as petrophilous (in Holdhaus' sense); the area-limiting factor for this species is chiefly thermal: the cold, resulting from the perpetual snow (see p. 465).

Holdhaus (1911a, p. 734; 1911b, p. 332) himself believes that petrophilous insects are not to be found in Fennoscandia and are probably completely missing from the region.** He thinks that the cause is the destructive effect of Quaternary glaciation and the generally weak dynamics of petrophiles, such that an interglacial or postglacial recolonization was prevented. In view of the detailed results obtained by Holdhaus one is not justified in considering the term "petrophilous" superfluous, as Brundin does (1934, p. 157).

It must therefore be assumed that the condition of the stony ground in central and southern European mountainous regions—chiefly in the Alps—exercises a much greater influence on the ground fauna than in our region. On the other hand, I would be convinced only by the positive results of experiments that even for markedly polyphagous animals, such as almost all carabids, the *chemical* composition of different kinds of rock is decisive.

*Palmén (1946, p. 25) has used the word in a different sense. He designated *Bembidion hirmocoelum*, which lives on stony river banks, "petrophilous."

**It is therefore incorrect for Holdhaus (1927–28, p. 948) to include *Pterostichus aethiops* among the petrophiles.

Among other comments, Holdhaus' remark (1911a, p. 733; 1911b, p. 331), that in the Alps and Carpathians "only such moraines as contain numerous very large block fields" possess a definite petrophilous fauna seems to confirm that even in these regions the *thermal* characteristics of the ground are decisive. I do not see why material transported by ice (not water!), that is, moraine, should be poorer in nutrient salt than the parent rock and the weathered soil, lying undisturbed over it. According to Kühnelt (1936, p. 12) even purely hygric conditions of the ground may bring about "petrophily."

Food and Feeding Habits

Carabidae, along with some closely related, chiefly aquatic families, are generally included taxonomically in the Carnivora or Adephaga. Hence they have been labeled *predatory* animals. This biological image pursues them throughout the entomological literature—pure as well as applied—and contrary observations (mostly in the genera *Amara*, *Harpalus*, and *Zabrus*) are generally considered exceptions.

I have not undertaken any systematic investigations on the food of Carabidae, but data collected from the literature and my own observations provide a picture which corresponds poorly with the usual concept of the predatory character of Carabidae.

The positive response of Carabidae to a *vegetarian diet* is most easily observed with specimens in captivity, which can be mostly (or exclusively) fed on bread. There is definite proof of *feeding on bread* in the case of the following 52 species:

Acupalpus consputus
A. exiguus
A. meridianus
Agonum dorsale
A. ericeti
A. krynicki
A. lugens
A. ruficorne
532 *A. sexpunctatum*
Amara aulica
A. equestris
A. ingenua
A. lucida
Bembidion aeneum
B. minimum
Brachynus crepitans
Bradycellus collaris
Calathus erratus
C. mollis
Carabus auratus*
C. cancellatus
C. coriaceus
C. granulatus
C. nemoralis
Cymindis angularis
C. humeralis
C. macularis
Harpalus aeneus
H. anxius
H. azureus
H. distinguendus
H. hirtipes

*The *Carabus* species according to Jung (1940).

H. melleti
H. neglectus
H. pubescens
H. punctatulus
H. puncticeps
H. rubripes
H. rufitarsis
H. rupicola
H. seladon
H. serripes
H. smaragdinus
H. tardus
H. vernalis
Lebia chlorocephala
Olisthopus rotundatus
Oodes gracilis
Panagaeus bipustulatus
Pterostichus anthracinus
P. lepidus
P. niger.

The least fastidious are *Brachynus* and *Harpalus serripes*. The former lived in captivity up to 17 months, the latter up to 32 months (!) fed only bread.

Most of these observations were made incidentally in connection with other experiments. The preponderance of the genus *Harpalus* in the list is chiefly due to the fact that I paid special attention to this genus for other purposes.

Instances where these insects were observed *feeding spontaneously on parts of plants** in nature are of greater interest. Further data on the plant part attacked in each case is superfluous here, since sufficient information can be obtained from Part I of this contribution and the Supplement to this part. The above evidence was obtained in the case of 45 species of our fauna (although some of it abroad). Mostly seeds and fruits were attacked; "v" = only vegetative parts of the plant. Only cases where feeding was proven (or as good as proven) were considered:

Amara aenea
A. aulica
A. bifrons
v *A. convexiuscula*
A. eurynota
A. familiaris
A. fulva
v *A. infima*
A. ovata
A. plebeja
533 *A. praetermissa*
A. quenseli
A. similata
v *Bembidion illigeri*
v *B. lampros*
v *B. monticola*
v *B. pygmaeum*
v *B. quadrimaculatum*
Calathus fuscipes
C. melanocephalus
Calosoma sycophanta
Carabus auratus
C. coriaceus
C. glabratus
C. nemoralis
v *C. violaceus*
Clivina fossor
v *Dichirotrichus pubescens*
Harpalus aeneus
H. calceatus

*In the few cases where especially juicy plant parts (melon, cherry) were attacked, it was perhaps due partly to thirst (for example in *Calosoma sycophanta*; but in connection with *Carabus* species see Jung, 1940).

H. distinguendus
H. griseus
H. pubescens
H. punctatulus
H. puncticeps
H. puncticollis
H. seladon
H. servus
H. tardus
v *Pterostichus cupreus*
P. lepidus
P. madidus
v *P. niger*
P. vulgaris
Zabrus tenebrioides.

Ninety-nine species were observed to consume animal food in the adult stage. In cases where the evidence was obtained only in captivity the name of the species is given in brackets:

(*Agonum dorsale*)
A. ericeti
(*A. lugens*)
(*A. ruficorne*)
(*A. sexpunctatum*)
Amara aenea
534 *A. alpina*
A. aulica
(*A. communis*)
A. curta
(*A. equestris*)
A. familiaris
(*A. ingenua*)
A. ovata
A. plebeja
Anisodactylus binotatus
(*Badister unipustulatus*)
(*Bembidion aeneum*)
Bembidion lampros
B. litorale
(*B. nigricorne*)
Bembidion nitidulum
B. obliquum
B. pallidipenne
B. rupestre
(*B. stephensi*)
B. varium
(*Brachynus crepitans*)
(*Bradycellus collaris*)
Broscus cephalotes
(*Calathus erratus*)
C. melanocephalus
(*C. mollis*)
Calosoma auropunctatum
C. inquisitor
C. reticulatum
C. sycophanta
Carabus arvensis
C. auratus
C. cancellatus
C. clathratus
C. convexus
C. coriaceus
C. glabratus
C. granulatus
C. hortensis
C. intricatus
C. monilis
C. nemoralis
C. problematicus
C. violaceus
Cicindela campestris
C. maritima
C. silvatica
Cychrus caraboides
(*Cymindis macularis*)
Demetrias imperialis
Dichirotrichus pubescens
Dromius agilis
*Dichirotrichus pubescens**

*Repetition in the German original—General Editor.

Dyschirius impunctipennis[†]
D. obscurus
D. politus
D. thoracicus
Elaphrus riparius
Harpalus aeneus
(*H. anxius*)
H. calceatus
Harpalus distinguendus
(*H. hirtipes*)
(*H. neglectus*)
H. pubescens
(*H. punctatulus*)
H. puncticeps
(*H. rubripes*)
(*H. rufus*)
(*H. serripes*)
(*H. smaragdinus*)
(*H. tardus*)
Lebia chlorocephala
L. crux-minor
(*Microlestes minutulus*)
(*Nebria livida*)
Notiophilus germinyi
Odacantha melanura
(*Omophron limbatum*)
(*Oodes gracilis*)
(*O. helopioides*)
Patrobus septentrionis
? (*Pristonychus terricola*
(*Pterostichus anthracinus*)
P. coerulescens
P. cupreus
P. punctulatus
P. vulgaris
Tachyta nana
Trechus quadristriatus
T. rivularis
Zabrus tenebrioides.

It is easy to summarize the above list as follows:

Animal diet: 99 species, 31 of which only in captivity. Vegetable diet: 85 species, 40 of which only in captivity. Exclusively animal diet: 53 species. Exclusively vegetable diet: 37 species. Mixed diet: 48 species.

535 It is evident from these figures that the Carabidae generally take vegetable diet. Moreover, among the 138 species actually studied here *no fewer than 48, i.e. 35%, can eat both animal and vegetable food.* I am convinced that this represents the normal situation in carabids, and that future more precise feeding experiments will demonstrate the generally *omnivorous* character of these insects.

Another aspect which is very important—not least for applied entomology—may be mentioned: Animal diet is not to be equated with predation. It can be easily observed that most carabids dare not attack healthy, uninjured prey; they flee before animals many times smaller than themselves. However, as soon as an insect, such as a worm, is injured, they seem to be attracted by the oozing body fluid and pounce on it. In all the species I studied in this connection this was true even where individuals of the same species were involved. In cultures with many *Harpalus* species, *Cymindis* species, *Brachynus*, *Agonum dorsale*, *Bradycellus collaris*, etc., I noticed that various species of Collembola and nonparasitic acarids always increased in numbers and were apparently not touched by the carabids. Gersdorf (1937, p. 80) mentioned that

[†]Generic name supplied by us—General Editor.

even *Carabus nemoralis*, which readily feeds on trampled snails, is never able to attack living slugs (also according to Jung, 1940). I have seen this species of *Carabus* in a keen tussle with a small *Lumbricus*, which it was unable to overpower. The two species of *Oodes* feed on all kinds of insects, but only after they have been seriously injured (Lindroth, 1943a, p. 115).

The response of most carabids to animal food is not really that of a predator but rather of a hungry scavenger. But they mostly avoid putrefying* matter and attack animals that are injured or have just been killed. If this is true, the importance of carabids in agricultural entomology as the generally accepted
536 effective enemies of insect pests of plants, is misplaced. Jung (1940) came to this conclusion with regard to the genus *Carabus*.

There are of course exceptions, among which species of *Calosoma* and *Cicindela* are the best known. The former are undoubtedly "useful" insects. Other carabid genera of our fauna whose members apparently consume chiefly animal food, and of which some represent true predators, are: *Agonum*, *Bembidion* (partly), *Calathus*, *Carabus*, *Cychrus*, *Dyschirius*, *Elaphrus*, *Notiophilus*, *Pterostichus* (partly). Predominantly plant-eating are mainly species of the genera *Amara*, *Harpalus*, and *Zabrus*, probably also *Bradycellus* among other "Harpalini." Some others are considered below.

These comments relate only to adults. Our knowledge of *the food of the larvae* is much poorer. This is regrettable since the presence of suitable food for the early, susceptible stages probably represents a greater problem than for the adult insects. It is therefore possible that the area of a markedly polyphagous beetle is limited by the more strict requirements in the food requirements of its larvae.

Carabid larvae of the Fennoscandian species for which definite data on diet were available number 48 species, only 13% of the fauna. These are the following species:

Amara aenea
A. consularis
A. curta
A. ingenua
A. ovata
Anisodactylus binotatus
Bembidion bipunctatum
Calathus melanocephalus
Calosoma auropunctatum
C. inquisitor
C. reticulatum
C. sycophanta
*Carabus*** *arvensis*
C. auratus
C. cancellatus
C. clathratus
C. coriaceus
C. granulatus

*Only species of *Carabus* seem to attack putrefying carcasses (Jung, 1940). In some other cases where carabids approach actually decaying carrion—if not just by chance—it might involve hunting for insect eggs, maggots of flies and the like.

**All *Carabus* larvae obtained by rearing from the egg (Bengtsson, 1927) are treated here as carnivorous. It is presumed that if, contrary to expectation, they had been fed on vegetable diet this would have been published.

C. hortensis	*H. pubescens*
C. intricatus	*Lebia cyanocephala*
C. monilis	*Licinus depressus*
C. nemoralis	*Metabletus truncatellus*
C. nitens	*Nebria brevicollis*
C. problematicus	*Oodes gracilis*
Carabus violaceus	*Pelophila borealis*
Chlaenius tristis	*Pterostichus anthracinus*
Cicindela campestris	*P. coerulescens*
C. silvatica	*P. cupreus*
Cychrus caraboides	*P. strenuus*
Dromius linearis	*P. vulgaris*
D. quadrinotatus	*Tachyta nana*
Dyschirius thoracicus	*Trechus quadristriatus*
Harpalus griseus	*Zabrus tenebrioides.*

No distinction could be made between the feeding experiments and observations made in nature, since there are few indications in the literature. In most cases the results of breeding experiments may have been involved.

The food of the larvae in almost every case was evidently animal matter. There are only five exceptions:

Amara aenea: "grain." But also designated "chiefly carnivorous."

A. ingenua: "Oats porridge."

Harpalus pubescens: "grain."

Pterostichus strenuus: "decomposed vegetable matter"; in addition, insects (Burmeister, 1939, p. 139).

Zabrus tenebrioides: chiefly leaves of cereal plants; in one case an *Anisoplia* larvae.

The feeding habits of carabid larvae—with the exception of the largest forms, such as *Calosoma*, *Carabus*, *Cicindela*—is an unexplored field. It is extremely difficult to draw general conclusions from the above meager list. Of course the idea may be justified that the larvae are far better disposed to an animal diet than the adults. But here too we must be careful not to designate the carabid larvae "predators." I wish to draw attention to the feeding experiments with the larvae of *Oodes gracilis* (Lindroth, 1943a, p. 115). Only living lumbricids were attacked, whereas all insects were eaten only when they were dead or seriously injured. Even the smallest living animals chase away carabid larvae.

538 Future precise studies will probably confirm that the larvae of carabids are invariably more dependent on animal food than the adults. However, in my opinion it will show that the larvae—like the adults—primarily attack dead and ailing animals, and also eggs and other defenseless stages. In choice of prey, with few exceptions, the larvae may be as polyphagous as the adults.

The feeding habit of a species assumes zoogeographical—area-limiting—significance only if there is a more or less considerable *specialization*. It is important to investigate whether some of the Fennoscandian carabids are dependent on very specific food—animal or plant—so that perhaps on this ground alone they are excluded from some parts of the Fennoscandian region.

An ecological group for which such an assumption could be made is the definite inhabitants of *cultivated land*. This chiefly includes a number of species of *Amara*, which are consistently found to occur on "weeds" favored by cultivation. The species of *Amara*, at least in the adult stage, are well known as pronounced plant eaters, chiefly seed eaters. They have been frequently observed nibbling at young pods of crucifers, so it is possible that they are associated with such plants due to their feeding habit.

I performed some experiments with *Amara ingenua*. These were carried out with a view to finding the cause of the rapid dispersal of this species in northern Fennoscandia during recent decades. A number of experiments first revealed that the explanation was not to be found in the increased use of synthetic fertilizers (p. 525). I therefore decided to test the appetite of the insect for different kinds of fruits and seeds.

Eight specimens of *Amara ingenua*, each isolated in a small glass dish, were provided with the same number and the same 13 types of nearly ripe fruits and seeds of the following plants, mainly "weeds." The experiment lasted 5 days; the diaspores were carefully studied every day and all traces of feeding were recorded. The diet of all 8 specimens is summarized here.

The experiment first of all shows the clearly polyphagous character of *Amara ingenua*. Of the 13 kinds of diaspores only 3 (*Anthriscus*, *Vicia*, *Viola*) were not attacked at all. On the other hand the insects showed a definite predilection for some of them, with *Polygonum aviculare* in first place. There is a complete correspondence with the natural occurrence of *Amara ingenua*, since this plant is almost always present. Its low height is especially advantageous, since the fruit can be easily reached by the insects. All the *Polygonum* fruits (with one odd exception) were completely eaten up. None of the other kinds of diaspore was. In the case of *Chenopodium album*, which according to the table is the next most favored, generally only the soft, juicy outer rind was nibbled, perhaps to satisfy thirst.

Since the species of *Amara* generally feed on young pods of crucifers, the same 8 individuals of *A. ingenua* were also offered a choice between fruits of *Polygonum aviculare* and green pods of *Capsella* and *Erysimum*:

Capsella bursa-pastoris 24 fruits, of which after 1 day
4 were consumed = 17%.

Erysimum cheiranthoides 24 fruits, of which after 1 day
3 were consumed = 12.5%.

539 **Table 33. Plants whose diaspores were attacked by 8 specimens of *Amara ingenua* during a 5-day experiment. F = fruit; S = seed**

Plant species	No. of diaspores/ specimens	No. of diaspores consumed on					Total, %
		1st day	2nd day	3rd day	4th day	5th day	
Anthriscus silvestris	2 F	0	0	0	0	0	0
Cerastium tomentosum	3 S	8	8	9	10	12	50
Chenopodium album	2 F	6	8	9	13	14	88
Cirsium arvense	2 F	2	4	8	8	9	56
Galeopsis sp.	2 F	0	0	0	1	1	6
Lapsana communis	3 F	1	6	9	9	12	50
Plantago major	5 S	1	1	1	1	1	3
Polygonum aviculare	2 F	9	15	15	15	15	94
Secale cereale	1 F	3	4	5	5	6	75
Sinapis arvensis	3 S	3	7	9	9	9	38
Thlaspi arvense	3 S	3	4	6	10	10	42
Vicia sepium	1 S	0	0	0	0	0	0
Viola arvensis	3 S	0	0	0	0	0	0

Polygonum aviculare 24 fruits, of which after 1 day
24 were consumed = 100%.

540 Like all other carabids *Amara ingenua* readily attacks dead or injured members of its own species. It would be interesting to expose these insects to a choice between animal and vegetable food. So each of 4 specimens was offered another, crushed, specimen along with 3 fruits of *Polygonum aviculare*. Three of the 4 specimens were observed attacking conspecific individuals during the night. Yet, on the next day 9 of the 12 fruits of *Polygonum* were found to have been nibbled on.

The following conclusion may be drawn: *Amara ingenua* is markedly polyphagous, taking both animal and vegetable food, but seems to prefer the latter, and feeds especially on seeds and fruits of "weeds" with a strong preference (as far as tested) for those of *Polygonum aviculare*. The answer to the question raised elsewhere (p. 630) as to why *Amara ingenua* has greatly extended its area in recent times, especially northward, may be this: The reclamation of land and the subsequent expansion of "weeds" provided new possibilities of

existence for the carabid in regions earlier occupied by forest and bog. The improved possibilities of anthropochorous dispersal have probably played only a subordinate role for this carabid which is capable of flight.

Attention may be drawn once again to the markedly *polyphagous* character of *Amara ingenua*. The species is in no way *bound* to *Polygonum aviculare*.

Other carabids more or less distinctly associated with particular plants, are the following:

Zabrus tenebrioides. The well-known "cereal ground beetle" is undoubtedly the most pronounced vegetarian among our carabids. It prefers *wheat* (*Triticum*), but also readily attacks rye (*Secale*), occasionally barley (*Hordeum*). The adults feed chiefly on the grain but the larvae eat young leaves. Occasionally the adult beetle, less often the larva, consumes animal food; the former was also observed feeding on a wild *Schedonorus*. Even if it turns out that *Zabrus tenebrioides* is completely dependent on the occurrence of wheat and rye, it is clear that its northern area limit is not dependent on its feeding habits.

Some other species also show a more or less clear association with *grasses*. Burrowing species have been occasionally found among roots of grass, and it was found in the case of *Amara infima* and *Harpalus rufus* that they nibble at them. But there is no ground for assuming that they are bound to a particular type of grass. The tendency of some animals of sandy ground to live in clumps
541 of grass is undoubtedly due chiefly to the more favorable moisture conditions there. The inclination is enhanced in dry weather.

Living in large fascicles of *Psamma* and *Elymus* along the seashore we find *Demetrias monostigma*, *Dromius linearis*, *D. longiceps*, *D. nigriventris*, and occasionally *D. sigma*. Nevertheless, none of these species is bound to this biotope. The attraction of loose sand for these non-burrowing insects is probably of microclimatic nature (p. 513). Since they cannot burrow themselves, it is natural for them to flee into the big fascicles of grass as the only available hiding place. Possibly they only find suitable prey there. The larva of *Dromius linearis* is stated to be a polyphagous carnivore; the closely (and ecologically) related *Demetrias imperialis* was observed feeding on a Collembola. At any rate the distribution of the above mentioned strand grasses cannot represent an area-limiting factor for any of our carabids.

In our region *Demetrias imperialis* and *Odacantha melanura* seem to have been observed only on shores where *Phragmites* grows. Whether a causal connection exists here is very uncertain. In central Europe *Odacantha* has been recorded more with *Typha*. Both species have been observed feeding spontaneously on Collembola. It is not possible that they are indirectly—through the prey (e.g. aphids)—bound to the plant. Since *Phragmites* has a wider geographical distribution in all directions than these two carabids, this does not represent an area-limiting factor.

More constant is the association of *Bembidion nigricorne* and *Bradycellus similis* with *Calluna*, which—as far as is known—are found only under this plant throughout their area (apart from accidental swarming flights of the *Bradycellus* species). *Carabus nitens* also apparently lives only where *Calluna* grows. Without experiments it is impossible to decide which factor is decisive here. However, the occurrence of *Calluna* does not determine the area limits of these species in Fennoscandia, since the plant has a much wider distribution. A strong attraction is exercised by *Calluna* on *Amara infima* too, and in the southern half of Fennoscandia on *Bradycellus collaris, Cymindis vaporariorum* and *Harpalus fuliginosus*. There is no question of the species actually being bound to it, except that one might like to speak of a southern "*Calluna*-race" in the last three cases (especially in the case of *Bradycellus collaris*).

542 *Amara aulica* likes to seek its food in the heads of *Compositae*, and most members of the *Harpalus* subgenus *Ophonus* in the umbels of *Umbelliferae*. In no case is there a dependence on a particular species of plant, probably not even a complete dependence on these families of plants. In any case the plants are more widely distributed in all directions than the cited carabids.

An isolated ecological group is bound to *trees*, the arboricoles, which play a prominent role in the tropics (for example, Darlington, 1943). In our region the number of carabids that spend their entire lives on living or dead trees is small: only 8 species. With one exception all of them belong to the genus *Dromius*. Since it must be especially interesting to determine whether one or other of our arboricoles is bound to a particular species of tree, their ecological distribution is tabulated in Table 34.

Table 34. Arboreal carabids of Fennoscandia. Only tree species occurring within the region are considered. Big cross = main occurrence; cross in parentheses = outside the region

	Larix	Picea	Pinus	Acer	Aesculus	Alnus	Betula	Corylus	Fagus	Fraxinus	Populus	Prunus	Pyrus	Quercus	Rosa	Salix	Sorbus	Tilia
Dromius agilis	—	+	+	—	—	—	+	(+)	+	+	+	—	(+)	+	—	(+)	+	+
D. angustus	—	(+)	**+**	—	—	—	—	—	—	—	—	(+)	—	—	—	—	(+)	—
D. fenestratus	—	+	**+**	+	—	+	+	—	+	—	+	—	—	(+)	—	—	+	+
D. marginellus	+	+	**+**	(+)	—	+	(+)	—	—	—	+	—	(+)	(+)	—	(+)	—	—
D. quadraticollis	—	(**+**)	+	—	—	—	—	—	—	—	—	—	—	(+)	—	—	—	—
D. quadrimaculatus	—	(+)	+	(+)	(+)	—	+	—	+	+	+	(+)	+	**+**	—	+	+	—
D. quadrinotatus	—	(+)	**+**	(+)	—	+	+	—	(+)	—	(+)	(+)	(+)	(+)	(+)	—	—	—
Tachyta nana	—	+	**+**	—	—	+	+	—	(+)	(+)	+	—	—	+	—	—	—	—

This survey shows that two species, *Dromius angustus* and *D. quadraticollis* (the latter found only once), have been found in Fennoscandia only on one
543 tree (*Pinus silvestris*). However, in other parts of their area these species also occur both on spruce (*Picea abies*) and on deciduous trees. In the case of *Dromius angustus*, the Fennoscandian localities are probably lococlimatically determined. This species is to be considered a relict, which continues to live only at thermally favored places. As a heat reservoir sand is pre-eminent, and among trees particularly *Pinus* grows on loose dry sand.

It is clear that none of our arboricoles is associated to one species of tree. It is not possible to determine why (with the exception of *Dromius agilis*) they prefer one particular tree (mostly *Pinus*). Probably the loose, scalelike structure of the bark of pine has a role here. As carnivores they may perhaps be dependent on a particular prey or may have a predilection for a particular kind. Occasionally, different ipids have been mentioned as species succeeding *Dromius* (Saalas, 1917, pp. 291 ff.), and *Tachyta* has regularly been found to inhabit their tunnels. However, in the diet of the latter Collembola have also been mentioned. The only adult of *Dromius* in which feeding seems to have been observed, *D. agilis*, is apparently markedly polyphagous (acarids, collemboles, aphids, "small larvae"). Characteristic is the small beetle "community" which in winter, together with *Dromius*, lives under the scales of bark at the base of the larger pines: *Hylurgops palliatus* Gyll., *Salpingus castaneus* Panz., and certain coccinellids, mainly *Adalia bipunctata* L. It is possible that these include the normal prey of *Dromius*, or of their larvae. In summer, when they live on the treetops (see Part I, p. 413), especially aphids seem to be the prey.

In conclusion, with regard to the eight arboricoles considered here, it may be stated that *none of them is bound to a particular species of tree*. All may occur both on conifers and on deciduous trees. It therefore seems to be ruled out that any of these eight species is dependent on a particular prey, since the tree-dwelling phytophagous animals are without exception bound to a more limited number of host plants.

Arboricoles of a more transient nature are two species of *Calosoma*: *C. inquisitor* and *C. sycophanta*, which spend their unusually short period of activity largely on trees, hunting for larvae and pupae. In *C. sycophanta* the larva also climbs. Otherwise this species holds little interest in the present context, since it is not dependent on any particular species of tree, nor on any particular
544 lepidopteran. On the other hand *C. inquisitor*, at least in our region*, seems to be bound to oak (*Quercus*). None of the records was made at places where oaks were not found nearby. Single records have also been made from other trees, which is natural for such a transient carabid. All records in large num-

*In central Europe *Calosoma inquisitor* appears in large numbers on *Carpinus* too (Holste, 1915). In captivity the larvae was fed with all kinds of lepidopteran larvae.

bers have been made in stands of oak. It is significant that in North America *C. inquisitor* is hard to naturalize, whereas this is not difficult in the case of *C. sycophanta* (Burgess and Collins, 1917). These findings are somewhat enigmatic, since the larvae of *Tortrix viridana* L. indeed form the chief prey of the carabid. On the other hand, the carabid may appear in fair numbers if there are plenty of geometrid larvae (for example *Erannis* = *Hybernia*), which can live on all kinds of deciduous trees. At any rate, *Calosoma inquisitor* does not quite reach the northern limit of the oak (in Finland *almost*: map, Fig. 61, p. 437), and not even the area limit of the prey (*Tortrix viridana* reaches Dlr; Benander, 1946, p. 16). Hence it can scarcely be contended that the northern area limit of the beetle is determined by its feeding habits.

Indirectly associated with particular trees is *Tachys bisulcatus*, which in our region lives in wet heaps of spruce bark, but in central Europe shows a broader ecological range. Some species show a marked predilection for beech forest: *Abax ater*, *Calathus piceus*, *Carabus coriaceus*, *Leistus rufomarginatus*. None of them is bound to the beech: in more southerly regions all of them are more eurytopic (*Carabus* also in central Scandinavia). But it is symptomatic to some extent that the relict-like northern outposts of *Abax ater* (southeastern Norway) and *Leistus rufomarginatus* (Vgl Råda) are found in the vicinity of the northernmost more extensive occurrence of *Fagus* (cf. Hjelmqvist, 1940).

This survey of the carabid species that have a more or less distinct association with one or other species of plant thus shows that an unfailing connection holds only between *Calluna* and *Bembidion nigricorne* and *Bradycellus similis*, possibly also between oak and *Calosoma inquisitor*. The true nature of these associations is unknown. On the other hand *Zabrus tenebrioides* is directly bound to species of grass (chiefly to cereals) on account of its feeding habit. However, in no case considered here does the beetle reach the area limit of
545 the plant concerned (the closest is *Calosoma inquisitor*). It must be concluded that *the distribution of a plant has area-limiting significance for none of the Fennoscandian carabids*.

The association, not with a particular species of plant, but with biotopes with a particular vegetation, is discussed in the section on "stenotopy and eurytopy" (pp. 563 ff.).

We now come to the more complicated question whether there are carabids that are dependent on quite special prey, whose area may be limited for this reason. The following cases suggest themselves in this connection (with regard to *Calosoma inquisitor* see above):

1. Genus *Dyschirius*. The species of this genus are well known as unfailing companions and hunters of the species of *Bledius*. Synopses on this have been provided by Sainte-Claire Deville (1924) and Burmeister (1939). Numerous observations have been made by Krogerus (1924, 1925a, 1925b, 1929) and Ellinor Bro Larsen (1936).

First one must be clear that not all species of *Dyschirius* are associated with *Bledius*. *D. globosus* and *D. helléni* are not associated with these animals at all. Three other species are more or less "blediophilous," but are not bound to this prey: *D. aeneus, D. lüdersi, D. septentrionum*. The last-mentioned species was observed by Krogerus (1924, p. 121) in tunnels of *Bledius longulus* Er., and the species often lives in association with many other species of the genus. But it occasionally also lives at places quite free from *Bledius*. The two first-mentioned species occur rarely together with species of *Bledius*. On the other hand species of *Heterocerus*, *Platystethus* or *Trogophloeus* mostly have localities in common and apparently represent the normal prey of this *Dyschirius* species.

We will now turn to the remaining species of *Dyschirius*, which have been observed without *Bledius* quite sporadically—perhaps only accidentally. These are the following species:

Dyschirius angustatus
D. chalceus
D. impunctipennis
D. intermedius
D. nitidus
D. obscurus
D. politus
D. salinus
D. thoracicus.

Nothing further seems to be known about the mode of life of *D. neresheimeri*.

A simple experiment was carried out separately with *D. obscurus* and
546 *D. thoracicus* (Experiments 105, 106, p. 84). In a deep dish with moist sand two small wire gauze cages were placed opposite one another, one empty and the other containing 6–8 specimens of *Bledius arenarius* Payk. A number of starved *Dyschirius* were introduced and their distribution in four equal sectors (A–D) was recorded after about 12 hours' exposure. The sectors were cut out at the time of recording (Fig. 5, p. 85). The following results were obtained:

	Sector				Total specimens
	A	B	C	D	
	Bledius cage	Without cage	Empty cage	Without cage	
Dyschirius obscurus	14	9	13	14	50
D. thoracicus	13	22	15	15	65

It seems to be justified to conclude that *Dyschirius* is not attracted to *Bledius* by a particular olfactory stimulus, in other words that its sense of smell is not especially directed toward this prey. The result is surprising because Ellinor Bro Larsen (1936, p. 125) found that a *Dyschirius* rubbed with the body fluid of a *Bledius* was at once attacked and eaten by its companions. However, I made a similar observation with *Stenus* (various species). Non-

injured individuals of this genus live undisturbed in cultures of *Dyschirius thoracicus*; but when a *Stenus* is decapitated, individuals of *Dyschirius* pounce on it and eat it up.

On another occasion I placed 3 healthy individuals of *Bledius arenarius* and a crushed fly in a culture of *Dyschirius obscurus*. After 10 hours the fly was found to be largely nibbled at, but the individuals of *Bledius* were untouched.

Like all other carabids, members of the genus *Dyschirius* also immediately attack an injured conspecific individual and eat it. At any rate it is clear that members of the genus *Dyschirius respond* especially *positively—with equal enthusiasm!—to the oozing body fluids of all kinds of insects* (*D. obscurus* was also tested on chironomids).

Even the *larvae* of *Dyschirius* are not specially disposed toward *Bledius* (chiefly its larvae). Both, Schiødte (1867, p. 503) and Ellinor Bro Larsen (1936, p. 126), observed them spontaneously consuming *Heterocerus*, including its larvae and eggs (in the first case the larva was found to belong to *D. thoracicus*).

This prompts the following conclusions: Members of the genus *Dyschirius* (at any rate *D. obscurus* and *D. thoracicus*) are not exclusively dependent on
547 *Bledius* for their food. They feed on all kinds of insects, especially injured or dead ones. But where they live, on account of the sparse occurrence or lack of tall vegetation, the fauna is extremely poor in species and consists chiefly of animals that can utilize *sand-algae* as food, primarily *Bledius* (Krogerus, 1925a, p. 4). *The primary prerequisite for the occurrence of a particular species of Dyschirius is the state of the soil* (p. 507). This must be suitable for digging tunnels, for which not only a particular particle size but also a definite, fairly constant moisture is necessary. *D. chalceus* and *D. salinus* also require NaCl. Which species of *Bledius*—or which other soil insects—are present there seems immaterial, provided they occur regularly and in sufficient numbers.

I found a good example of the factors effective for the distribution of *Dyschirius* on the seashore of Vbt Byske (July 15, 1936), where *Bledius arenarius* was unusually common everywhere on the barren sandy shore. Living along with it, although not associated with it, were found *Dyschirius obscurus* and *D. thoracicus*. The former was found alone, closer to the waterline, in *finer* and *moister* sand. That *D. obscurus* prefers fine-grained sand was found both in nature (Krogerus, 1932, p. 164) and experimentally (p. 507). It is also more resistant to exposure to water than *D. thoracicus* (Krogerus, 1932, p. 237). The almost obligatory association between *D. obscurus*—and also of *D. impunctipennis*—and *Bledius arenarius* is undoubtedly due largely to the identical requirements of these three species in the above-mentioned context with respect to the kind of sand.

On the other hand *D. thoracicus* is more eurytopic (occurring on coarser and on loam-mixed sand) and was found along with more species of *Bledius* (for example, Krogerus, 1923, p. 121).

It is very significant that the 5 species of *Dyschirius not* associated with

Bledius (see above), live all at places with a more or less rich and taller vegetation, where the insect fauna is much richer in species, so that they are not dependent on a particular prey.

In conclusion it may be considered inconsequential which factor is primary, sand or *Bledius*, since both must be present! Strictly speaking, neither of them is actually the decisive *area-limiting* factor for any species of *Dyschirius*. More correctly, the disjunct occurrence of shoreline with suitable sand and *Bledius*
548 is decisive (see sand map, Fig. 77, p. 510). Of prime importance is the ability of *Dyschirius* to find and to colonize these places, which are so far certainly inhabited only by a small fraction of the possible species. *Factors related to the immigration history—in particular, time—hold the key.*

Since *Asaphidion pallipes* has also hardly been observed at places free of *Bledius* it is possible to consider this species as identical with *Dyschirius* in its feeding habit. But the adult does not burrow.

2. *Brachynus crepitans*. For three years I spent much time on unsuccessful experiments to clarify the feeding habit of this species. The adult beetle is very easy to please: it can be fed on all kinds of crushed (but not living) insects, on individuals of *Lumbricus*, etc. Some beetles were given only bread for more than a year.

The habits of the *larva* are completely unknown. But the attempt has been made to find out why *Brachynus crepitans* is, so to speak (in our region almost always), consistently in the company of *Agonum dorsale*, particularly since the larval stage of the North American *B. janthinipennis* Dej. has been found a parasite of the pupa of a gyrinid species (*Dineutes*) (Dimmock and Knab, 1904).

It was therefore necessary to study the behavior of *Brachynus crepitans* toward the *Agonum* species as precisely as possible. At least in captivity *Brachynus* behaves passively toward the succeeding species, whereas *Agonum* shows strikingly "friendly" behavior. Often it positions itself next to *Brachynus* and ardently rubs its back and the sides of the prothorax and elytra fore and aft, like a cat, against various parts of the body of *Brachynus*. Of course *Agonum* also shows similar behavior toward its own kind, even toward dead objects. At any rate this does not indicate that the *Agonum* species is in any way dependent on *Brachynus*; over wide areas, for example in Skåne, it lives alone.

During the "cleansing ritual" *Brachynus* remains passive. Besides, a simple experiment in the substratum gradient apparatus (Experiment 104, p. 84) was used to establish that it is not attracted to *Agonum* by the olfactory stimulus. In 5 boxes the two species were distributed as follows:

549	*Brachynus*	*Brachynus*	*Agonum*	*Brachynus*	*Brachynus*
	6 specimens	6 specimens	10 specimens	6 specimens	6 specimens

The *Agonum* box was covered with thin cloth to prevent entry and exit. After 3 replicates of the experiment and each 3-day exposure the following distribution

figures were obtained:

Brachynus	*Brachynus*	*Agonum*	*Brachynus*	*Brachynus*
17	19	—	17	19

The distribution was thus identical.

The two species of beetle were maintained in common culture for several months without attacking each other.

On two occasions I also obtained numerous *Brachynus* larvae in the cultures (see Supplement). However, it was impossible to find suitable food; all kinds of crushed insects, individuals of *Lumbricus*, bread, etc. were left untouched and the larvae all died without perceptible growth.

The larvae behaved passively toward *Agonum dorsale*. I also reared two larvae of *Agonum dorsale* from the eggs for almost 3 weeks together with *Brachynus* larvae, without observing any attack. When finally (on July 8) one *Agonum* larva pupated, the last *Brachynus* larvae were already dead 3 days. The only combination not tested was *Brachynus* larva with *Agonum* pupa. Yet it may be justified in ruling out any parasitism: First, the *Agonum* pupa is too small (dry body weight of the adult beetle 4.08 mg as against 6.96 mg for *Brachynus*: mean value for 10 specimens of each from Öland*). Second, it appears too late in the summer, since oviposition by the two species takes place at about the same time. *Brachynus* and *Agonum dorsale* apparently do not have parasitic (or feeding habit) relationship with one another. They are just a rare example of two species with nearly identical ecological requirements, and have been considered as such above (pp. 59–64).

The larval biology of *Brachynus* thus remains unsolved. Several biotopes (in Upl, Ögl, Öld) where the beetle occurs frequently were carefully dug up
550 and sifted during those three summers without a trace of a larva. The other insect inhabitants of these places were collected and noted, and some, with the right size and time of appearance in the larval or pupal stage, were offered to freshly emerged *Brachynus* larvae, but without success. Further description of this repeated failure is superfluous. But it seems to me that all this favors the view that the larva of *Brachynus crepitans*, like that of *B. janthinipennis*, is a monophagous parasite. If I finally think of ants this is to be considered only a weak, private hypothesis.

So at present it is not possible to decide whether the feeding habit of the larva is a decisive area-limiting factor for *Brachynus crepitans*. Perhaps one must ask which other insect ("the host") could possess the extremely characteristic distribution of *Brachynus*.

3. Species of *Lebia*. Analogous cases exist here. Abroad the larva not only of the notorious *Lebia scapularis* Fourc. has been found as a monophagous

*According to a letter from Darlington, *Brachynus janthinipennis* Dej. (auct.) is about 7.5 mm long, and its host *Dineutes americanus* Say (auct.) 10–11 mm. Since the gyrinids are known to possess a sticky body, the difference in body weight in favor of *Dineutes* is probably still greater.

ectoparasite (on *Galerucella luteola* Müll.)* but also of the North American *Lebia grandis* Hentz (on *Leptinotarsa decemlineata* Say) (Chaboussou, 1939). The hosts in these cases therefore consist of grown-up larvae or pupae of chrysomelids. The adults of some American and African species of *Lebia* seem to be monophagous predators on chrysomelids as well (Chaboussou, l.c.).

So far, there are no definite observations in this regard on the three species occurring in Fennoscandia. Burmeister's contention (1939, p. 190) that the larva of *Lebia crux-minor* feeds on the larvae of *Galeruca* and *Chrysomela* is based—as far as I can see—on assumptions by others (for instance, Blunck, 1925, p. 37). However, the assumption is probably correct. In Fennoscandia *L. crux-minor* is found nearly always at places inhabited by *Galeruca tanaceti* L. In northern Sweden this species along with *Chrysomela marginata* L., is the only chrysomelid of a suitable size. On the other hand, the above mentioned
551 *Chrysomela* species is so rare in parts of southern Sweden that it cannot be the only host. If *Lebia crux-minor* is bound to a chrysomelid as a monophage this must be *Galeruca tanaceti*. The presumed host has a much wider distribution than *Lebia* (especially in Norway). Hence, in Fennoscandia the feeding habit as an area-limiting factor of this species is involved at the most only slightly.

The adult *Lebia chlorocephala* is found to be rather polyphagous in captivity (for instance, it eats aphids and also bread). But in nature it was found regularly associated with species of *Chrysomela*, especially *C. varians* Schall. (see also West, 1947, p. 17) and was also observed feeding on its larvae, so that a constant association of the *Lebia* larva with this prey can be presumed. If the distribution of the two species (*Chrysomela* according to the *Catalogus*, 1939) is compared there is a good correspondence inasmuch as *C. varians* advances northward in Finland much farther than in Sweden. On the other hand this species is so far unknown in southern Österbotten, in Hälsingland and on Bornholm, regions where numerous records of *Lebia* have been made. *C. fastuosa* Scop. lives in the first of these regions and the *Lebia* adult was found feeding on its larva in central Europe. But in Hls and on Bornholm even this species seems to be missing. We may conclude from this that *Lebia chlorocephala*, if as larva it is dependent on species of *Chrysomela*, which seems probable, it nevertheless cannot be monophagously bound to a single species. So the feeding habit can hardly have an area-limiting role for this species either.

In the case of the third species of *Lebia*, *L. cyanocephala*, no association was established with a particular prey. If Xambeu's data (1898, p. 175)** are

*Burmeister (1939, p. 191) also mentions *Galerucella lincola* Fbr. as the host of *Lebia scapularis*, without citing his source. Chaboussou (1939) includes only *Galerucella luteola*.

**Erroneously cited by Blunck (1925, p. 37).

reliable, on the contrary it can be argued that the larva of *L. cyanocephala* is a thoroughly polyphagous predator.

4. Snail-eating species. Only two species seem to be obligatory snail-eaters, *Cychrus caraboides* and *Licinus depressus*, the latter at least in the larval stage. The former of these is said to feed almost exclusively as adult on snails in the shell, for which purpose the slender anterior part of the body with the elongated head is especially suitable (see figure in Burmeister, 1939, p. 47). Jeannel's assumption (1941–42, p. 989) that the larvae of *Licinus* feed on
552 snails, which seemed highly probable in view of the strong resemblance with the snail-eating larva of *Dicaelus* from North America (Dimmock and Knab, 1904, p. 26), has been confirmed. On June 15, 1947, on Öland, Greby alvar, I observed a half-grown larva of *Licinus depressus* busy in eating a small snail (*Vallonia costata* Müll., det. N. Hj. Odhner). This snail is widely distributed across the southern half of Sweden inhabiting a much larger area than the *Licinus*.

Until we establish, first, whether the two above-mentioned species (at least as larvae) are able to live *exclusively* on snails and, second, whether they are associated with a particular species of snail, which I do not believe, it is impossible to evaluate the area-limiting significance of this special mode of life.

Moreover, some species of *Carabus*, especially *C. coriaceus*, have a strong inclination to feed on snails (both without and with the shell). However, no species is bound to this mode of life.

5. Some other species with special modes of life may be specialized in their diet.

Tachyta nana seems to live under the bark of trees only where there are abundant tunnels of ipids, and is said to feed in all stages chiefly (not exclusively) on these insects. However, there is no dependence on any particular species of ipid, so the area-limiting significance of this feeding habit must be slight. For similar tree-dwelling species of *Dromius* see above (p. 542).

The food of *Miscodera arctica* is not known. However, the constant occurrence of byrrhids (especially *Byrrhus fasciatus* Forst. and *Cytilus sericeus* Forst.) in the habitats of *Miscodera* is suggestive, and it is possible that these animals represent their normal prey. But the Fennoscandian distribution of these byrrhids is almost universal, so the thinning out of *Miscodera* in the south and the general limits of the area cannot be explained on the basis of feeding habits.

The anthropobiont "domestic animals" *Pristonychus terricola* and *Sphodrus leucophthalmus* often live in association with species of *Blaps* and may be dependent on them or at least favored by them.

6. A very special "association" is formed by the *inhabitants of animal nests*. Fennoscandian carabids are associated only with the nests of rodents and of
553 *Talpa* (in England the development of *Bembidion harpaloides* was observed in a *Garrulus* nest).

Trechus discus and *T. micros* seem to be completely dependent on mammalian nests (for a similar dependence of other *Trechus* species on rodents, assumed by Danish entomologists, see Part I, p. 668, footnote). Probably the two species of *Bembidion* in the subgenus *Ocys, B. harpaloides** and *B. quinquestriatum*, also have an obligate association with animal nests, details of which remain to be clarified. *Trechus quadristriatus* shows a predilection for rodent dwellings but is not bound to them. For *Agonum quadripunctatum* see Part I (pp. 86–87) and p. 528 above. How careful one must be in saying that a species of beetle is bound to animal nests purely on the basis of its more or less regular occurrence there, is clearly shown by Sokolowski (1942, for instance, p. 186) for Catopidae.

It is not easy to decide whether the dependence on animal nests, chiefly that of *Trechus discus* and *T. micros*, is due to feeding habit or not. Possibly these species are secondarily dependent on other nidicolous small animals for food. It should not be forgotten that animal nests also represent a very peculiar biotope with respect to their thermally well-balanced *microclimate*, as is evident from the detailed studies by Nordberg (1936, pp. 60 ff.). At any rate, not only in Fennoscandia but in the rest of Europe (Borchert, 1938, p. 7, Map 50) the almost identical distribution of the two species of *Trechus* seems to show clearly that their areas are regulated by one and the same factor. This factor cannot be the distribution of their most important common host, *Arvicola amphibius*, whose distribution is almost pan-Fennoscandian. On the other hand it would certainly be strange if just the thermal factor had the same effect (an identical distribution) for two species, one of which (*T. discus*) hibernates as a larva and the other (*T. micros*) as an adult. The question stands: only this much is established, that the areas of *Trechus discus* and *T. micros* are not limited by the occurrence of their presumptive hosts.

554 Summing up the consideration of *food as an area-limiting factor* for the Fennoscandian carabids, we find that a decisive role can be ascribed to it at the most in exceptional cases.

A particular species of plant which could at least indirectly exercise an influence through feeding habits seems indispensable for at most three species, namely *Calluna* for *Bembidion nigricorne* and *Bradycellus similis*, and perhaps also the oak for *Calosoma inquisitor*.

A particular species of animal (*Galeruca tanaceti*) can be taken, most probably, as necessary only for *Lebia crux-minor*. For good reasons was a similar, but as yet unknown, dependence also assumed for *Brachynus crepitans*. Most species of *Dyschirius*, *Lebia chlorocephala* and *Tachyta nana* are more or less "oligophagous" carnivores; for a few others only hypotheses in the same direction are possible. Two species of *Trechus* are apparently bound to small

*Horion (in litt.) is of the view that *Bembidion harpaloides* is not constantly associated with animal nests (see Supplement).

mammals, likewise possibly two species of *Bembidion*.

In the few cases where a more or less constant feeding habit association was established between a carabid and a plant or animal species, the "host species"—with *Calosoma inquisitor* as partial exception—is so much more widely distributed than the carabid dependent on it *that the area-limiting factor must be of different nature*. One reason that carabids offer an unusually suitable subject for zoogeographical research is that in them the feeding habit factors have a subordinate role, so that other factors, less specialized thus more significant, are isolated and their effect brought out. These are foremost: the *climate and the dynamical characteristics of the animal*, and secondly the characteristics of the soil.

Competitors and Enemies

There is hardly an ecological factor whose effect in nature is more difficult to determine than *the competition between organisms having identical or similar requirements of life*. In most plants as well as in sessile animals it is to a large extent purely a "struggle for space" (combined with the requirements of food,
555 oxygen, light, etc.). In the case of freely moving animals *the struggle for food* assumes first place.

It is generally contended that competition is strongest among species taxonomically closely related to one another, since it may be expected that these are also more or less related in their feeding habit. Thus Elton (1946) undertook a statistical analysis of the animal "communities" of a large number of biotopes of the most diverse types, and found that the number of animal genera represented within each biotope (s. l.) *by one single species* is larger than what might be expected from a purely accidental distribution of the fauna. Apart from the fact that the figures Elton gives can be interpreted in a different way (Williams, 1947; see below), attention may also be drawn to the following: Whether or not taxonomically closely related forms—designated as species or otherwise—are competitors for food, an ecological difference, at the very beginning, must strongly favor the functional separation of a newly originated type from "the old species." *Ecological insolation*, rendering hybridization difficult, must help to originate a genetically fixed new form (see, among others, Crombie, 1947, p. 64). If Elton's view that closely related forms mostly live separately is correct, this need not mean that they compete with one another, but that ecological difference is the primary requirement for their development as physiologically different entities.

However, Williams (1947) has opposed Elton's view (1946) that in identical conditions of competition the mean number of species per genus in each geographical or ecological region remains unaltered, independent of the size of the species stock, and that therefore any decline in the number of species must be ascribed to the effect of increased competition among members of

the same genus. Williams (also 1944) found that the number of genera with 1, 2, etc. species form a logarithmic series, which becomes more distinct, the larger the material in hand. A test of this method on the entire Fennoscandian carabid fauna (Diagram 53) gives a fairly good correspondence between the
557 empirically and logarithmically calculated figures.* From this it follows that in samples poorer in species a considerable purely mathematical reduction must be expected in the number of species per genus.

As an example, to enable us to test statistically the effect of "intrageneric" competition (among members of the same genus), the carabid fauna of some riverside biotopes of Norrbotten (Lindroth and Palm, 1934) and Värmland (Palm and Lindroth, 1937) may be selected. These studies may be especially suitable for the present investigation because banks represent narrowly delimited, comparatively small biotopes where the effect of possible competition should be clearly evident.

Table 35 gives the calculated mean number of species per genus and the same value for the total of 6 or 12 samples from each riverside biotopes studied, for the entire carabid fauna of Nbt and Vrm respectively, and finally for the carabid fauna of the whole Fennoscandian region. These empirical figures were compared with those calculated logarithmically according to Williams' method. It is evident from this comparison that the mean number of species of carabid genera of these riverside biotopes is everywhere greater than what might have been expected. If any conclusions can be drawn from this they should rather indicate a selection *in favor of* the association of taxonomically closely related forms rather than the opposite! This result agrees with that obtained by Williams (1947).

However, mention must be made of a factor that might lead to increase of the mean number of species per genus in special biotopes—such as the riversides considered. At such places, where more or less extreme factors exist—for instance, sparsity or absence of taller vegetation, big fluctuations in the water level, etc.—a particular constitution (physiology) of the animals is often called for. For instance, species of *Dyschirius* and *Bembidion* are especially suited for life on banks. However, there is a larger number of genera that are excluded for these very reasons. *In extreme biotopes the number of genera diminishes.* Consequently—speaking from the viewpoint of competition—more "space" becomes available to species of the few genera that are represented there. So even with unchanged conditions of competition more species per genus may be expected.

It is therefore best not to take the calculations according to Williams'
559 method as proof for a favored association between members of the same genus, but on the other hand it does not seem possible to confirm the contrary theory

*These and all other mathematically calculated figures in this section were worked out by Fil. Lic. Leo Uskila.

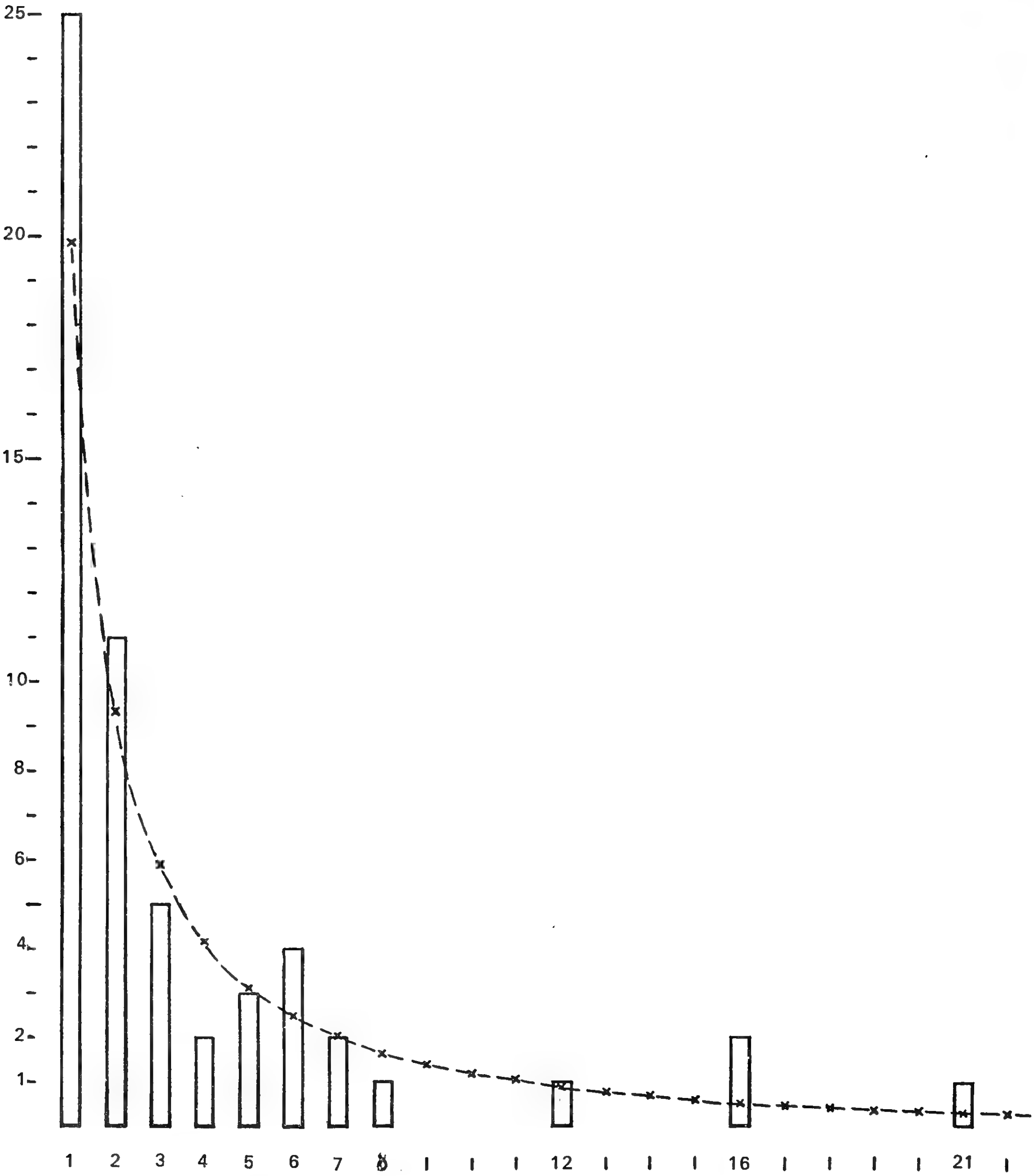


Diagram 53. Number of genera with 1, 2, etc. species constituting the Fennoscandian carabid fauna (61 genera, 362 species).

Curve based on Williams' figures (1944, 1947). Outside the diagram one genus each with 30, 32, 39 and 65 species respectively.

proposed by Elton (1946), using statistical methods.

The association of numerous closely related species of carabids is not at all unusual. A good example is the well-known *Harpalus* locality, visited by many collectors, in Öld Stora-Rör (Lindroth, 1948c, p. 44). Here, on the edge of a thick *Calluna* cover which to the east is fringed by open sand, 12 species were found in one day to occur together (*H. aeneus*, *H. anxius*, *H. hirtipes*, *H. melancholicus*, *H. neglectus*, *H. picipennis*, *H. rufitarsis*, *H. serripes*, *H. servus*, *H. smaragdinus*, *H. tardus*, *H. vernalis*), i.e. more than 50% of the known Fennoscandian species of *Harpalus* s. str. Some of them (especially *H. anxius* and *H. smaragdinus*) were present in very large numbers. In 1910 all the species were collected by Sandin near Stora-Rör; it must be a fairly stable "community."

Numerous more or less synanthropous species of *Amara* have also been constantly found together. In many places in southern and central Sweden the following species can be found together *in a few square meters* of sandy or gravelly soil in a sunny situation, with rich vegetation of *Artemisia vulgaris*, *Arctium* and tall species of *Rumex*, *Polygonum aviculare*, *Stellaria media*, etc.; *A. apricaria*, *A. aulica*, *A. bifrons*, *A. consularis*. *A. eurynota*, *A. familiaris*, *A. fulva*, *A. ingenua*, *A. municipalis*, *A. ovata*, *A. similata*. Also often found living together are *Calathus* (on Öland and Gotland always *C. ambiguus*, *C. fuscipes*, *C. mollis*), *Ophonus* (*O. melleti*, *O. punctatulus*, *O. rupicola*, often also *O. azureus*, occasionally *O. seladon*). In the winter half-year we find living under the bark of trees several species of *Dromius* (especially *D. fenestratus*, *D. marginellus*, *D. quadrimaculatus*, *D. quadrinotatus*).

On the basis of both statistical study and the field experience of entomologists one gets the impression *that the competition for food among different carabids has no significant role*. At any rate, the idea that closely related species represent especially serious competitors seems baseless. For this reason I am inclined to ascribe Krogerus' finding (1947, p. 45), that species of the muscid genus *Coenosia* occur as biotope dominants, so to speak as vicariads, rather to an undertermined abiotic environmental difference than to a competitive relationship.

560 I know of only one case where there seems to be effective competition among species of carabids. The stronger competitor here is *Carabus nemoralis*. In the Fennoscandian region it is undoubtedly a comparatively late immigrant (p. 632) which is still in the process of dispersal. To the extent that it has greatly increased in numbers—especially around cities—other species of *Carabus* have become noticeably scarcer. This is especially true of *C. hortensis*, which likes the same biotopes as *C. nemoralis*: sparse woodland, for instance, parks, with moderately moist soil, preferably with an admixture of gravel.

It would certainly be interesting to study the competition between *Carabus nemoralis* and *C. hortensis* experimentally. No explanation may be forthcoming without that. But attention is drawn here to one aspect that may perhaps

Table 35. Distribution of numbers of carabid species of different genera in some riverside biotopes in Norrbotten and Värmland. Comparison is made with the total carabid fauna of these two provinces and with the carabid fauna of Fennoscandia as a whole

	Acupalpus	Agonum	Amara	Asaphidion	Bembidion	Blethisa	Broscus	Calathus	Chlænius	Cicindela	Clivina	Cychrus	Dromius	Dyschirius	Elaphrus	Harpalus	Leistus	Loricera	Metabletus	Nebria	Notiophilus	Patrobus	Pelophila	Perileptus	Pterostichus	Trechus	Trichocellus	Number of species	Number of genera	Mean number of species per genus: Empirical	Mean number of species per genus: Calculated (after Williams)	Deviation
NORRBOTTEN																																
Karungi		4	3		4						1			1	2	1		1				1	1		4	1		24	12	2,00	1,50	+ 0,50
Över-Torneå		6	1		7			1			1			2	2	1		1		1		1	1					25	12	2,08	1,52	+ 0,56
Vitsaniemi		4	1		6	1					1			1								2	1		6			23	9	2,56	1 48	+ 1,08
Över-Kalix		5	1		8			1			1			1	2	1		1	1				1		2			25	12	2,08	1,52	+ 0,56
Neder-Kalix		3	2		3			1			1			2			1	1							2	1		17	10	1,70	1,40	+ 0,30
Älvsbyn		6			9									3	2	1		1		1	1		1		1	1		27	11	2,46	1,55	+ 0,91
6 Localities		7	6		12	1		1			1			3	2	1	1	1	1	1	1	2	1		7	1		50	18	2,78	1,95	+ 0,83
Carabid fauna of Norrbotten																												115	32	3,59	2,93	+ 0,66
VÄRMLAND																																
Fastnäs				2	10		1				1			2	1					1					1			19	8	2,38	1,40	+ 0,98
Likenäs		3	1		8		1				1			1	1	1				1					1			19	10	1,90	1,40	+ 0,50
Vingäng		3		1	7			1	1					2	2	1								1				19	9	2,11	1,40	+ 0,71
Höljes		2			4			2				1		1	2	2	1	1		1	2	1			5	2	1	28	15	1,87	1,57	+ 0,30
Långflon		1	2		9			2			1			1	1						2				2			21	9	2,33	1,44	+ 0,89
Sälje		5			8						1			2	2					1						1		20	7	2,86	1,42	+ 1,44
Ekshärad		1	3	1	4			2			1		1			2	1					1			2	1	1	21	13	1,62	1,44	+ 0,18
Holsby		1		1	7						1			1	1				1	1					2			16	9	1,78	1,35	+ 0,43
Olsäter		2		2	5			2			1	1	1	1			1			1	1	1			2	1		22	14	1,57	1,46	+ 0,11
Deje		1		1	11			2		1				2	1			1		1								21	9	2,33	1,44	+ 0,89
Forshaga	1			1	9			1			1			2						2		1			1	1		20	10	2,00	1,42	+ 0,58
Karlstad		2		1	9						1			2	1	1	1			1		1			2	2		24	12	2,00	1,50	+ 0,50
12 Localities	1	8	5	2	19		1	3	1	1	1	1	1	3	2	3	2	1	1	2	3	2		1	8	2	1	75	25	3,00	2,35	+ 0,65
Carabid fauna of Värmland																												183	41	4,46	3,83	+ 0,73
Carabid fauna of the whole of Fennoscandia																												362	61	5,93	—	—

be useful. An important biological difference between the two species is that *nemoralis* hibernates as an audit, *hortensis* predominantly as a larva. Moreover, *nemoralis* is an unusually hardy, insect, which goes hunting on frost-free nights in the winter half-year. It needs to be found out whether the larva of *hortensis* is not more susceptible to cold: in spring it wakes up to full activity later than the *nemoralis* adult. Perhaps during this transitional period it is a defenseless prey for the beetle.

At any rate it might turn out that quantitative fluctuation in the populations of the two species of *Carabus* is not due to simple competition for food, but that *nemoralis* is actually an active enemy of *hortensis*.

Gersdorf (1937, p. 78) surmises that in Germany there is similar competition between *Carabus auratus* and *C. cancellatus*, in favor of the former. Renkonen (1944, pp. 88 ff.) posits a possible competition between *Philonthus quisquiliarius* Gyll. and *P. micans* Gr.

Evidently the carabids have numerous enemies. On the other hand there are remarkably few enemies that unilaterally specialize in this prey. The best-known at present is *Methoca ichneumonides* Latr., belonging to the family Thynnidae, which is an unfailing enemy of *Cicindela* larvae (Adlerz, 1916, pp. 299 ff.). However, throughout our region this parasite seems to be rare.

Larvae of *Calosoma* and *Carabus*, as well as those of *Nebria brevicollis* and *Pterostichus vulgaris*, are occasionally parasitized by numerous larvae of the
561 proctotrupid genus *Phaenoserphus*—probably always *P. viator* Hal. (Kieffer, 1914, p. 29; Holste, 1915, p. 419; Burmeister, 1939, pp. 32, 34, 140). It is possible that the "ichneumonid" mentioned by Lengerken (1921, p. 33) being parasitic on *Carabus silvestris* Panz. also belongs here.

More numerous are the parasites found on carabid adults. In the gut and in the body cavity of the larger species (*Carabus, Broscus, Pterostichus niger*) *gregarines* are very often found, which probably belong to the species *Monocystis legeri* L.F. Blanck (Delkeskamp, 1930, pp. 18–20). They never appear to endanger the life of the host, but if they enter the body cavity they apparently cause castration.

Endoparasitic nematodes (genus *Rhabditis*) have been found both in adults of *Calosoma sycophanta* and in a larva of *Carabus monilis* (Burgess, 1911, p. 71). It could not be ascertained whether they are harmful for the host. *Gordius* worms were observed by Gersdorf (1937, p. 31) once in *Pterostichus oblongopunctatus* and once in *P. vulgaris*; according to Burmeister (1939, p. 37) *Gordius aquaticus* L. lives in *Carabus coriaceus*. These worms occur in carabids only occasionally.

Some *tachinid* maggots are endoparasites capable of causing the death of various larger carabids. *Viviania cinerea* Fall. has been found in several species of the genera *Amara*, *Broscus*, *Calathus*, *Carabus*, *Harpalus*, *Pterostichus*, and *Zabrus* (J.C. Nielsen, 1909, p. 72; 1918, p. 253; Lundbeck, 1927, p. 286; Audcent, 1942); *Freraea gagathea* R.D. (*albipennis* Zett.) was found

in *Carabus monilis* and *harpalus pubescens* (J.C. Nielsen, 1916; Lundbeck, 1927, p. 120), and finally *Weberia pseudofunesta* Villen. (*curvicauda* auct.) in *Amara aulica* and *Harpalus pubescens* (Lundbeck, 1927, p. 117), possibly also in *H. aeneus* (J.C. Nielsen, 1909, p. 76).

In North America a *braconid* (*Microctonus carabivorus* Mues.) is known to be parasitic on the adult of a carabid (*Galerita* sp.) (Muesebeck, 1931, pp. 16–17). It is possible that in Europe, too, related species have a similar mode of life.

Very often *acarids* are found attached to carabids, occurring in enormous numbers, especially in cultures. They can cause death at least of larvae, but on the other hand may have no role in nature. These casual parasites may belong to various genera (Burgess, 1911, p. 70; Delkeskamp, 1930, pp. 20–21.) Obligatory parasitic acarids were found on the coxae of *Carabus granulatus*
562 and *Pterostichus niger* (Gersdorf, 1937, p. 31), but especially under the elytra of species of *Carabus* (Family Canestrinidae; Delkeskamp, 1930, p. 22; Gersdorf, l.c.; Sellnick, 1939, p. 1304) and on hygrophilous species of the genera *Agonum*, *Bembidion* and *Pterostichus* (Parasitiformes: Sellnick, l.c.). taxonomically these parasites are very little known. Their effect on the host seems to be insignificant.

An idea of the relatively little importance of parasites living on carabids is provided by the fact that in my fairly extensive cultures of adults of numerous species, some of them lasting over long periods, I was never able to attribute the death of an individual to the effect of parasitization. Besides acarids—both casual and obligatory parasites—there were only ectoparasitic fungi of the Family Laboulbeniaceae (Lindroth, 1948b), occurring fairly abundantly. These, too, do not appear to endanger the life of the hosts.

We therefore find that—as far as is known—no single parasite (perhaps with the exception of some Laboulbeniaceae) is specific to a particular species of carabid, and of the few species of lethal parasites none seems to occur regularly and in large numbers. The statement is justified that the carabids—especially in comparison with Lepidoptera, Diptera, and other families of beetles, such as Chrysomelidae and Curculionidae—are parasite-free to an unusually high degree.

On the other hand they undoubtedly have numerous enemies of another kind, designated as predators. The most dangerous are certainly various birds. Often the excreta of birds consist almost entirely of elytra and other hard parts of beetles. Such excreta may originate especially from members of the crow family (Corvidae). Careful studies carried out by Notini (1943) on the diet of the hooded crow (*Corvus cornix* L.) showed that carabids—especially the diurnal species—constitute a major part of the diet (cf. also Burgess, 1911, p. 70). Other birds feeding on carabids are also mentioned in the literature (Krogerus, 1932, p. 176; Gersdorf, 1937, p. 30, Burmeister, 1939, pp. 27, 32, 129).

Other enemies of carabids are the fox (*Canis vulpes*; Lengerken, 1921, p. 32; Burmeister, 1939, pp. 32, 43), "mice" (Burmeister, l.c.), the mole (*Talpa*; Burmeister, l.c.), shrews (*Sorex*; Lengerken, l.c.), and above all probably the badger (*Meles taxus*), which has a strong inclination to feed on the
563 larger, chiefly nocturnal species (Notini, 1948, p. 119). Of course bats (Chiroptera) also feed on night-flying species. Toads (*Bufo*) are also mentioned by Lengerken and Burmeister (l.c.).

Gersdorf (1937, pp. 30–31) notes that the larger staphylinids (*Staphylinus, Philonthus)* hunt for carabids; they seem to possess an important weapon in the form of a paralyzing poison (especially mentioned in *Paederus*). Carabids also attack one another, especially injured, diseased or still teneral individuals, as well as eggs and larvae (p. 535).

This brief survey of the enemies—parasites and predators—of carabids has shown that the number of species involved is high. However, it is striking that these enemies are little specialized. None of them is dependent on one species of carabid for prey. It is evident that these enemies, and I am inclined to put birds in the first place, may bring about a reduction in the size of populations. On the other hand it does not seem possible to consider this as an effective area-limiting factor.

The view expressed above (p. 554) in considering the feeding habits is thus confirmed and can be expanded as follows: *Biotic factors play a subordinate role in the distribution of carabids*; *decisive are the abiotic existence factors* (*climate and soil*) *and the dynamical factors*.

Stenotopy and Eurytopy

It is a proud moment for the experienced field entomologist when, on an excursion, well beforehand—from as far away as possible—he can point out to his younger colleague, in a calm voice, the locality of one or other of his favorite animals. Such prophecies come true in remarkably many cases. Often even "the prophet" is surprised, for he is not always clear why he expected just this or that species there. However, on numerous collecting trips he has learned to associate certain definite environmental factors with some particular animal species, until the psychic channel is so fixed that a particular combination of environmental factors in nature automatically directs the thought to a particular species of animal.

564 In this way the field entomologist gradually and almost unknowingly acquires an idea of the conditions essential for life of the more or less stenotopic species, those more or less closely associated with a particular biotope, such as those identified by the entomologist chiefly from the vegetation.

The world "stenotopic" (opposite: "eurytopic") is nevertheless a highly relative term, not only in the extent to which an obligatory association with a particular biotope is required or not, but chiefly according to whether the

term “biotope” is interpreted in a narrower or a wider sense. The biotope “comprises sections of the living space, which are identical in the essential conditions of the requirements of life for organisms existing there, the life forms, that are adapted to these conditions, and thereby differ from other locations” (Hesse, 1924, p. 141). It is evident from the examples cited that Hesse interprets the term rather narrowly—with full justification: slimy, sandy, gravelly and rubbly shores (of the sea) are designated as different biotopes.

For those terrestrial surfaces that are included under the term “biotope,” therefore, as far-reaching a correspondence as possible may be required in the following most important features: condition of soil (particle size, secondarily also the chemistry), moisture, insolation, and—arising chiefly through the combined effect of the above factors—the vegetation. On the other hand it is difficult to judge the extent to which certain requirements of a biotope can be ascribed to the climate (microclimate), since localities that must be considered as belonging to the same biotope (for example, a *Sphagnum fuscum* bog, a sandy *Calluna-Pinus* forest) may lie in very different climatic regions.

Strictly speaking, then, only species that inhabit a particular biotope exclusively and at all times is stenotopic. However, in practice a few restrictions are justified. Accidentally occurring individuals in alien biotopes may be chance migrants, winged insects being especially common. Even if they come to reproduce at such places, the species need not be denied stenotopy unconditionally, provided this does not result in permanent colonizations in alien biotopes. Species that undertake more or less regular migrations can be stenotopic nevertheless, if the reproduction (larval development) is biotope-bound. Examples of this are to be found chiefly among the riparian carabids, which in winter often live quite far from water (Lindroth, 1943; H. Krogerus, 1948).

565 No species is eurytopic in the broadest sense, i.e. “inhabiting all biotopes.” However, to be justly called eurytopic an animal must not exhibit any predilection for a well-defined biotope. The most eurytopic of all Fennoscandian carabids may be *Dyschirius globosus. Bembidion lampros* could possibly vie with it for this rank. Examples of more limited eurytopes are: *Pterostichus diligens* (eurytopic hygrophilous species), *Bembidion rupestre* (eurytopic shore species), *Harpalus aeneus* (eurytopic dry-meadow species), *Calathus micropterus* (eurytopic forest species), etc.

It is not possible here to enumerate all the more or less distinctly stenotopic carabids. The most pronounced cases, which also deserve detailed study from the purely zoogeographical viewpoint, seem to be following:

In hardwood forests

Abex ater
Calathus piceus
Calosoma inquisitor (p. 543)
Leistus rufomarginatus
Nebria brevicollis

In hardwood forest swamps

Acupalpus consputus — *Badister unipustulatus*
Agonum krynicki — *Bembidion clarki*
Badister Sodalis

In forest bogs ("Bruchwaldmoore")

Trechus rivularis

In open hypnum moss bogs ("Braunmoore")

Agonum consimile — *Elaphrus lapponicus*

On *Sphagnum* quaking land (not *S. fuscum*)

Agonum munsteri

In *Sphagnum fuscum* bogs

Agonum ericeti — *Dyschirius helléni*

On peat soil

Bembidion humerale

In dry tundra

Diachila polita — *Trichocellus mannerheimi.*
Pterostichus middendorffi

566 In sandy fields and "steppe soil" (see "limestone species," pp. 115 ff.). Furthermore:

Amara infima — *A. spreta*
A. quenseli — *Pterostichus lepidus.*

On *Calluna* heath (p. 541).

On riverbanks with varied sized soil particles (pp. 508 ff.).

On the shores of eutrophic lakes (p. 528).

It is now clear that the zoogeographical significance of the greater or lesser stenotopy of a species is completely dependent on the more or less frequent occurrence of the required biotope. In a continuously wooded area—such as most of Fennoscandia—a forest-bound species such as *Calathus micropterus* may occur almost ubiquitously, and for similar reasons, *Bradycellus similis*, apparently dependent on *Calluna*, has a wide area in the southwest. Fastidious species such as, among those mentioned above, *Agonum ericeti*, *A. munsteri*, *Trechus rivularis*, must have a correspondingly disjunct area. Clear examples of this kind were found by comparisons between the sand and loam maps (Figs. 77, 78, pp. 510, 511) and in the distribution of some species especially sensitive to the ground material (pp. 512 ff.).

Nevertheless it is particularly important that fragmentation of the habitable area is a great hindrance to dispersal, a question considered below.

The cause of stenotopy is doubtful. We can only presume that a markedly stenotopic species has unusually fixed requirements of the environmental factors. In general it must remain undecided whether a single factor or a combination of factors is decisive, or whether finally we must look for a complex "holocoenotic standard factor" (Friederichs, 1930, p. 109).

This may be exemplified by the riparian species. They are undoubtedly ripicolous, since they have definite *moisture* requirements. The choice between different types of shore seems to be determined chiefly by the mechanical (including hygric) characteristics of the ground material, especially *particle size.* Moreover, some species inhabit only open shores, *exposed to sun*. They are to a large extent dependent on the *vegetation*, which also influences the soil
567 mechanically and chemically. Some riparian species live only at the sea-side, and may be dependent on the *saline content* of the soil. *Thermal* contrasts are chiefly represented on the one hand by the banks of springs and rapid brooks (with stable, low temperature) and on the other hand by those of shallow, slightly warmed ponds and lakes. Finally reference should also be made to the availability of sufficient *food*, which is a particular problem, for instance, for the species of *Dyschirius* (p. 545).

Especially informative are cases where a species inhabits diverse biotopes in different parts of its area. In Part I of this contribution numerous examples of this kind were provided, where the mode of life of a carabid in central Europe may be different from that in our region. A survey of the clearest cases shows the following:

a) In central Europe more eurytopic (not only on sand; p. 513):

Bembidion nigricorne	*Dromius angustus.*

b) In central Europe more hygrophilous:

Agonum dorsale	*Leistus ferrugineus*
Dromius linearis	*Stomis pumicatus*
D. melanocephalus	*Synuchus nivalis.*

c) In central Europe more along *running* waters:

Agonum marginatum	*Bembidion velox.*
A. ruficorne	

d) In central Europe more on the seashore:

Bembidion saxatile

e) In central Europe more in bogs:

Agonum obscurum	*Notiophilus germinyi*
Amara infima	*Olisthopus rotundatus*
Bembidion obliquum	*Patrobus assimilis*
B. rupestre	*Pterostichus diligens*
Bradycellus similis	*Trichocellus cognatus.*
Carabus clathratus	

In the case of the two last-mentioned species the transition to more humid biotopes is already noticeable in southern Sweden.

f) In central Europe more in woodland:

Bembidion schüppeli
B. semipunctatum
568 *Carabus arvensis*
C. convexus
C. problematicus
Harpalus rufitarsis
Neberia salina.

These 6 seemingly different groups can easily be combined under a common criterion: In the northern parts of their area these species live in open habitats (f), on drier soil (b), also on standing, fresh water (c, d) and not exclusively in bogs (e), i.e. *in wamer places*. The conclusion, expressed as a general rule, would run as follows: *At the limits of its area an animal or plant species often tends toward stenotopy, which is microclimatically determined.* The best examples are on the one hand the southern carabids, which at their northern limit become sand-inhabiting (p. 513) or limestone insects (pp. 188 ff.), and on the other hand the northern species, which toward their southern limit tend to inhabit bogs.

Types of Development

Detailed studies on the annual development of the nordic carabids were carried out by S.G. Larsson (1939, 1940). He saw that these phenomena have considerable zoogeographical significance.

With few exceptions (chiefly, a 2-year development), the nordic carabids can be divided into 2 main types, which Larsson designates *spring breeders or spring insects* ("*F*") *and autumn breeders or autumn insects* ("*H*"). For various reasons it seems advantageous to use the designations *imago hibernators* (*I*) and *larval hibernators* (*L*) respectively. First, June, when most carabids copulate and oviposit, at least in Fennoscandia, is hardly spring; second, the hibernating stage—at any rate from the zoogeographical and ecological viewpoint—is the most important expression of the development type; third, it might be pointless to try to introduce the symbols "F" and "H"—which are abbreviations of German words—into international usage, whereas imago (I) and larva (L) are already in general use.

In addition to species that more or less clearly represent either of the two types of development, there are those which are very unstable, regularly
569 hibernating both as imago and in the larval stage. These are here designated 0 (null). On the other hand in our region it never seems to happen that a carabid has more than one generation per year; the use of the expressions "spring generation" and "autumn generation"—especially for several species of *Amara*—by Burmeister (1939) is probably due to a misunderstanding (see Part I, p. 128, footnote).

The results I obtained in connection with the types of development of a series of species, which differ from Larsson's are not especially cited here,

but information was provided against the species concerned in Part I ("Specific Part") of this contribution. Partly our different results are simply due to the fact that the carabids in more northerly regions have different conditions of development (it is uncertain whether genetically determined or not); in other cases, in my opinion, Larsson has based his conclusions on too little observation material.

The *larval hibernators* (*L*) in Fennoscandia comprise a strikingly small number of (at most) only 72 species (20% of the fauna). Those which also hibernate more or less regularly as imago are in parentheses below. The species of *Cicindela*—with a 2-year development—are also included. Some doubtful cases are indicated with a question mark.

569–570 ? *Aëpus marinus*
(*Amara apricaria*)
A. aulica
A. bifrons
(*A. brunnea*)
A. consularis
A. convexiuscula
(*A. cursitans*)
Amara equestris
A. fulva
A. fusca
A. majuscula
(*A. municipalis*)
A. praetermissa
Asaphidion pallipes
Bembidion lunatum
(*Bradycellus harpalinus*)
? (*B. verbasci*)
(*Broscus cephalotes*)
Calathus ambiguus
(*C. erratus*)
(*C. fuscipes*)
(*C. melanocephalus*)
C. mollis
C. piceus
(*Carabus coriaceus*)
(*C. glabratus*)
C. hortensis
C. monilis
(*C. violaceus*)
(*Cicindela campestris*)
(*C. hybrida*)
(*C. maritima*)
(*C. silvatica*)
(*Cychrus caraboides*)
(*Cymindis angularis*)
(*Cymindis humeralis*)
C. macularis
(*C. vaporariorum*)
Dichirotrichus pubescens
Dolichus halensis
Harpalus calceatus
(*H. griseus*)
(*H. melancholicus*)
(*H. pubescens*)
(*H. puncticeps*)
(*H. rufus*)
(*H. smaragdinus*)
Leistus ferrugineus
L. rufescens
L. rufomarginatus
(*Masoreus wetterhalli*)
(*Nebria brevicollis*)
(*N. gyllenhali*)
N. livida
(*N. salina*)
Notiophilus germinyi
(*N. pusillus*)
(*Olisthopus rotundatus*)
(*Patrobus assimilis*)
(*P. atrorufus*)
Pterostichus lepidus

(P. niger)
(P. vulgaris)
Sphodrus leucophthalmus
Synuchus nivalis
Trechus discus
? *T. fulvus*
(T. obtusus)
T. quadristriatus
T. secalis
Zabrus tenebrioides.

570 Among the "O-species" with irregular hibernation—a fairly arbitrary group—I include 17 species (4.7%). For the markedly northern species this is tentative: clarification of their development must be left to future detailed studies. Probably the 2-year development is due to the short summer in the fjeld regions and the far north. It is even possible that the ability of some species (for instance, *Notiophilus aquaticus*) to switch to this kind of development is a characteristic of *great positive selection value* (already assumed for Lepidoptera by Valle, 1933, p. 98).

The suggested "O-species" are:

Abax ater
Agonum obscurum
? *Amara alpina*
A. quenseli
? *A. torrida*
? *Bembidion grapei*
Carabus problematicus
Harpalus latus
H. punctatulus
H. quadripunctatus
H. rubripes
? *Nebria nivalis*
Notiophilus aquaticus
Omophron limbatum
Patrobus septentrionis
Pristonychus terricola
? *Pterostichus madidus.*

571 Among species that normally hibernate as imago, there are finally some which in *exceptional cases* may also hibernate as larvae (possibly as pupae). This has been established in at least the following 29 species, but evidently is also possible in some others:

Agonum fuliginosum
A. lugens
A. thoreyi
*Amara communis**
A. lucida
A. nitida
Bembidion aeneum
B. bipunctatum
B. transparens
Brachynus crepitans
Bradycellus collaris
Calathus micropterus
Carabus clathratus
Dromius agilis
D. angustus
Dromius linearis
Harpalus azureus
H. hirtipes
H. melleti
H. tardus
H. vernalis
Lebia chlorocephala
Loricera pilicornis
Pterostichus diligens
P. gracilis
P. minor

*"Irregularities" in *Amara communis* will easily be understood if it turns out to be a species complex (see Supplement).

P. nigrita	*Trechus rubens.*
P. oblongopunctatus	

The zoogeographical significance of the two types of hibernation (in addition to the mixed type) may be in the first place the different requirements of *climate.* The situation was considered above (p. 475) in the relevant section. Thus the type of development of the insect indirectly becomes an *important area-limiting factor.*

Besides, it has a considerable indirect effect on the dynamical characteristics of the insect, namely the ability of the species to utilize the possibilities of hydrochorous transport during the *winter half-year.* These questions were considered in connection with the insular faunas (pp. 205 ff.).

Finally, a small observation which supports the view that the hibernating stage of carabids is not a casual function of external conditions (the prevailing autumn conditions), but is probably determined genetically (but see also
572 Uvarov, 1931, pp. 105 ff.). In crossing experiments with macropterous and brachypterous *Pterostichus vulgaris* which emerged on August 31, five larvae, which were fed on pieces of *Lumbricus*, grew rapidly and soon went through the first molt, whereupon they again ate heartily until their new skin was stretched tight. They were kept indoors throughout. Yet without there being any symptom of disease it was impossible to make the larvae undergo the second molt. They stopped eating and each of them made a small cave in the soil, in which they lay motionless—apparently "waiting" for the winter.

Dynamic Factors

The distribution of an animal or a plant species depends on where its requirements for life are met and on the possibility of the species seeking out such suitable regions and permanently colonizing them. These two groups of factors were clearly distinguished for the first time by Ekman (1922, p. 308), and were termed respectively *existence ecological and dispersal ecological* (Swedish: "spridningsekologiska") factors. In the present contribution—for the reasons given above (p. 13)—the terms *existence factors and dynamic factors* are preferred.

The preceding section was devoted to the existence factors. They operate through the interaction between the characteristics of the insect and those of the environment.

At first sight the dynamic factors seem unilaterally dependent on the characteristics of the animal—on its capability of dispersal. This is incorrect. *Passive* modes of dispersal often play a greater role than active ones. And the effect of both is determined by the natural *barriers against dispersal.*

Like the preceding section, this one is also written continually distinguishing between the "characteristics of the insect" and the "characteristics of the environment."

Theoretically it could be argued that if only enough time were available, each species would finally colonize the entire habitable area. The point is of no real interest. The duration of (geomorphologically, climatically, etc.)
573 comparatively stable geological periods is too short. However, the effect of the modes of dispersal is at any rate directly proportional to the available time.

The last section of this book is devoted to the importance of time as a zoogeographical factor—the history of the Fennoscandian fauna.

Flight Capacity and Wind Dispersal

One of the most interesting characteristics of carabids as objects of zoogeographical study is the fact that there are both species capable of flight and flightless species, and even species (50) where only certain individuals are capable of flight (p. 337). Hence a study of the dynamical significance of flight capacity and the zoogeographical exploitation of aerial transport by these insects should be very fruitful.

In our carabid fauna the constantly flightless species form only a small component. They can be considered brachypterous, but on the other hand should not be called apterous (wingless), since at least rudiments of the hind wings are always present. The following 49 species (13.6% of the fauna) are constantly flightless:

573–574 *Abax ater*
Aëpus marinus
(*Agonum ericeti*)
Badister sodalis
(*Bembidion dauricum*)
B. unicolor
? *Broscus cephalotes*
Calathus fuscipes
C. micropterus
Carabus arvensis
C. auratus
C. cancellatus
C. convexus
C. coriaceus
C. glabratus
574 (*C. granulatus*)
C. hortensis
C. intricatus
C. menetriesi
C. monilis
C. nemoralis
C. nitens
C. problematicus
C. violaceus
Cychrus caraboides
Cymindis angularis
C. humeralis
(*Demetrias monostigma*)
Diachila polita
Dyschirius globosus
D. helléni
Elaphrus angusticollis
Harpalus vernalis
Leistus ferrugineus
L. rufescens
Licinus depressus
Metabletus foveatus
Patrobus assimilis
P. atrorufus
Pristonychus terricola
Pterostichus aethiops
P. fastidiosus
P. madidus
P. middendorffi
Stomis pumicatus
(*Trechus fulvus*)
(*T. obtusus*)
T. secalis
Trichocellus mannerheimi.

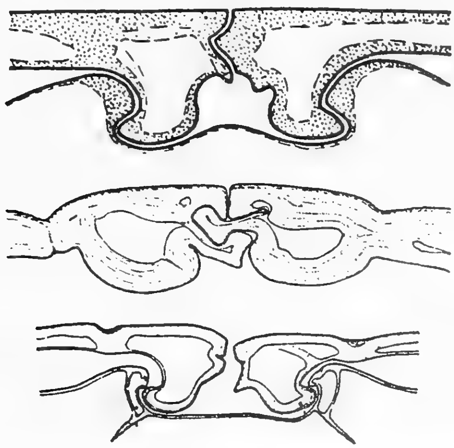
In the case of the 6 species in parentheses (see Part I) macropterous individuals are found in other regions but in our region they do not seem to be dimorphic. This is conceivable for *Badister sodalis* and *Elaphrus angusticollis*, where the only moderately reduced wing rudiment shows great variability (see p. 338).

Nevertheless it is doubtful whether *Broscus* is to be considered among the functionally brachypterous species. The wings seem always to be fully developed, with a strong, apical reflexed part; the flight musculature, which was studied in several specimens, shows some degenerative characteristics. On the other hand even the first glimpse gives an impression that the elytra are firmly ankylosed immediately behind the scutellum, possibly even fused. But this impression is corrected by a dissection. It has been found (Fig. 81a) that the elytra are not fused and are also not anchored to each other in the way described by Corset (1931) in some constantly brachypterous species (such as *Carabus coriaceus*, Fig. 81b). On the other hand, the downward bent sutural margins are anchored in the posteriorly converging sharp longitudinal grooves of the metascutellum still more firmly than in *Calathus erratus* described above

(p. 350). Moreover, the elytra, behind the part sketched in the figure, are firmly joined through sharp sutural ridges; these ridges belong alternately to the right elytron (in the middle) and to the left elytron (in front of and behind the middle). All these structures together form an effective locking mechanism, which could be released only by strong lateral movements and by lowering the strongly chitinized longitudinal folds bounding the longitudinal grooves of the metascutellum on the outside. I have not been able to decide whether such movements are possible. Good examples of structurally much simpler sutural margins in carabids capable of flight are provided by some species illustrated by Corset (1931) (Fig. 81c). However, it should be noted that ankylosis of all kinds between the elytra may often look even in constantly brachypterous species (for example *Bembidion unicolor*, *Metabletus foveatus*, *Patrobus atrorufus*). According to Sharp (1913) the elytra of *Pterostichus madidus* are not constantly ankylosed.

If *Broscus* were actually capable of flight, it would be strange that this has never been observed in such a large, conspicuous and widely distributed beetle. It is also significant that this beetle is missing from the sandy outer islands in the Gulf of Finland, where it would undoubtedly find the best possibilities of existence. The occurrence in Gotska Sandön can perhaps be explained by transport through water (p. 285). In light of the above discussion we may be justified in including *Broscus cephalotes*—at least provisionally—among the flightless species.

The only two other doubtful species are *Leistus ferrugineus* and *rufescens*, whose wings are comparatively well developed, but smaller and weaker than



a

b

c

Fig. 81. Transverse section through the anterior part of the suture of elytra.

a—*Broscus cephalotes* (about 1 mm behind scutellum, posterior view); b—*Carabus coriaceus*; c—*Penetratus rufipennis* Dej. (b and c after Corset, 1931).

in *L. rufomarginatus* (see Part I). At any rate it seems to be ruled out that *L. ferrugineus* could be capable of flight. Both species are considered here as constantly brachypterous.

Carabids *constantly capable of flight*, numbering 263 species (73%), constitute the major part of our fauna.* It might have been more prudent to
576 designate these "constantly macropterous," since the flight capacity can be established beyond doubt only by observations or experiments.

Definite records of flight are available for 177 species (for details, reference may be made to Part I and to the Supplement to this part). In the following list, species with flight records only outside the region are given in brackets. On the other hand there is no reason to distinguish between species observed flying spontaneously in nature and those impelled to fly only by exposure to sunlight, warming up, etc.

Species demonstrably capable of flight**

Acupalpus consputus
A. dorsalis
A. exiguus
A. flavicollis
A. meridianus
Agonum assimile
(*A. bogemanni*)
A. consimile
A. dolens
A. dorsale
A. gracile
(*A. gracilipes*)
(*A. livens*)
(*A. longiventre*)
A. lugens
(*A. marginatum*)
A. micans
A. mülleri
A. piceum
A. quadripunctatum
A. thoreyi
A. versutum
A. viduum
Amara aenea
A. apricaria
(*A. aulica*)
*A. bifrons****
A. communis
A. consularis
(*A. crenata*)
A. eurynota
A. familiaris
A. fulva
A. ingenua
A. interstitialis
A. lunicollis
A. majuscula
A. montivaga
A. municipalis
A. ovata
A. plebeja
A. praetermissa
A. similata
(*A. spreta*)
A. tibialis
Anisodactylus binotatus

*"Constantly capable of flight" here covers dimorphic species that occur exclusively in the macropterous form in Fennoscandia.

**Dimorphic species that have been observed flying are mentioned on p. 337.

***Caught in the flight-apparatus by Ossiannilsson (see Supplement).

577 (*Asaphidion flavipes*)
A. pallipes
(*Badister bipustulatus*)
B. dilatatus
B. peltatus
B. unipustulatus
Bembidion argenteolum
B. articulatum
(*B. biguttatum*)
B. bipunctatum
(*B. dentellum*)
B. difficile
B. doris
B. femoratum
(*B. fumigatum*)
B. hasti
B. hirmocoleum
B. hyperboraeorum
B. illigeri
B. lapponicum
B. litorale
B. lunatum
B. lunulatum
B. minimum
(*B. nitidulum*)
B. obliquum
(*B. pallidipenne*)
B. prasinum
B. punctulatum
B. quadrimaculatum
(*B. quinquestriatum*)
(*B. ruficolle*)
B. rupestre
B. siebkei
B. stephensi
(*B. striatum*)
(*B. tibiale*)
578 *B. tinctum*
B. varium
Bembidion velox
Blethisa multipunctata

Bradycellus similis
B. verbasci
Calathus ambiguus
(*Calosoma auropunctatum*)
(*C. denticolle*)
(*C. inquisitor*)
C. sycophanta
Chlaenius nigricornis
C. quadrisulcatus
(*C. sulcicollis*)
C. tristis
Cicindela campestris
C. hybrida
C. maritima
C. silvatica
(*Clivina collaris*)
C. fossor
Demetrias imperialis
Diachila arctica
(*Dichirotrichus pubescens*)
*D. rufithorax**
(*Dolichus halensis*)
Dromius agilis
D. angustus
D. fenestratus
D. longiceps
D. marginellus
(*D. quadraticollis*)
D. quadrimaculatus
(*D. quadrinotatus*)
(*Dyschirius aeneus*)
? (*D. impunctipennis*)
D. lüdersi
(*D. nitidus*)
(*D. obscurus*)
D. politus
D. thoracicus
Elaphrus cupreus
E. riparius
Harpalus aeneus
H. anxius

*Caught in the flight-apparatus by Ossiannilsson (see Supplement).

H. calceatus
H. distinguendus
(*H. frölichi*)
H. griscus
(*H. hirtipes*)
H. latus
H. melleti
H. pubescens
H. punctatulus
(*H. puncticeps*)
H. rubripes
H. rufitarsis
H. rupicola
(*H. seladon*)
(*H. serripes*)
(*H. smaragdinus*)
(*H. tardus*)
H. winkleri
Lebia chlorocephala
L. crux-minor
L. cyanocephala
Loricera pilicornis
Microlestes minutulus
Miscodera arctica
Nebria brevicollis
(*Omophron limbatum*)
Oodes gracilis
O. helopioides
Patrobus septentrionis
Pelophila borealis
(Perileptus areolatus)
Pogonus luridipennis
Pterostichus adstrictus
(P. aterrimus)
P. coerulescens
P. cupreus
(P. gracilis)
(P. niger)
P. nigrita
(Sphodrus leucophthalmus)
Stenolophus mixtus
(*Tachys bistriatus*)
T. bisulcatus
Trechus discus
T. micros
T. quadristriatus
T. rubens
Trichocellus cognatus
(*Zabrus tenebrioides*).

Accordingly 86 constantly macropterous species are left, for which there is no clear proof of flight capacity. Enumeration seems superfluous. Some of them show almost definite proof of flight capacity by their occurrence, for instance, in drift material on the seashore, but there is no such proof in other cases.

However, comparison of the relative wing size of these species with their closest relatives provides grounds for a more or less definite verdict on the functional ability of these organs. Perhaps it would be possible to calculate a "flight index" based on the relationship between wing surface and body weight (cf. Prochnow, 1921–24, p. 564), to which at least within each genus some significance could be attached as a "measure of flight capacity"—assuming the
579 flight mechanism to be identical. But my attempt to establish this index failed due to the great variability in the body weight even of the same individual (on account of uptake of food and water, presence of eggs in the female, etc.); the dry weight cannot be used. The calculated length or surface relationship between the hind wings and the elytra is of no use either; compare the difference between an *Odacantha* and a *Lebia*!

It is left to one's judgment whether the development of the hind wings of a particular carabid enables it to fly or not. Actually there are very few cases admitting of real doubt: I will mention only *Agonum ruficorne, Amara equestris, Odacantha melanura* and *Pterostichus oblongopunctatus*, which were nevertheless, probably correctly included among constantly macropterous species.

In line with the above, the Fennoscandian carabids are divisible into the *following dynamic groups*:

Constantly macropterous species, demonstrably capable of flight: 177 = 48.9% of the fauna.

Constantly macropterous species, without records of flight: 86 = 23.7% of the fauna.

Dimorphic species (p. 337): 50 = 13.8% of the fauna.

Constantly brachypterous species: 49 = 13.6% of the fauna.

The first two groups can naturally be combined, although they were kept separate in considering the dynamics of the insular faunas (pp. 198 ff.). It can be assumed that the first group ("m," p. 206) includes the best, most regular fliers, and represents the most mobile elements of the fauna.

Otherwise the different carabids capable of flight are by no means dynamically on a par.

First of all we have a very small group of species for which flying is as common an activity as running, particularly in the sunshine; all of them are markedly heliophilous. These species use their wings chiefly to hunt their prey, to escape from danger, etc. In our region, these *obligatory* fliers include only members of the genus *Cicindela* and the subgenera *Bracteon* and *Chrysobracteon* of *Bembidion*, making the following 9 species:

Bembidion argenteolum	*Cicindela campestris*
B. lapponicum	*C. hybrida*
B. litorale	*C. maritima*
B. striatum	*C. silvatica.*
B. velox	

580 Most of the other carabids capable of flight use their wings only in exceptional cases. Often one may have to conduct many unsuccessful experiments with exposure to sun, artificial light, heat (in dry and in humid air), before at best, flight is induced. One gets the definite impression that the decisive factor is not the external conditions but the disposition of the insect, "the inclination to take flight." First of all it is clear that the insects *do not fly in all seasons*.

From this viewpoint I have prepared a synopsis (Diagram 54) of the monthly distribution in the region of all specimens of carabids (excluding *Cicindela*, *Bracteon*, and *Chrysobracteon*) *observed spontaneously flying*. It was found advantageous to divide the material into two groups: *Imago hibernators* (which hibernate only exceptionally as larvae), and more or less regular *larval hibernators* (see p. 568).

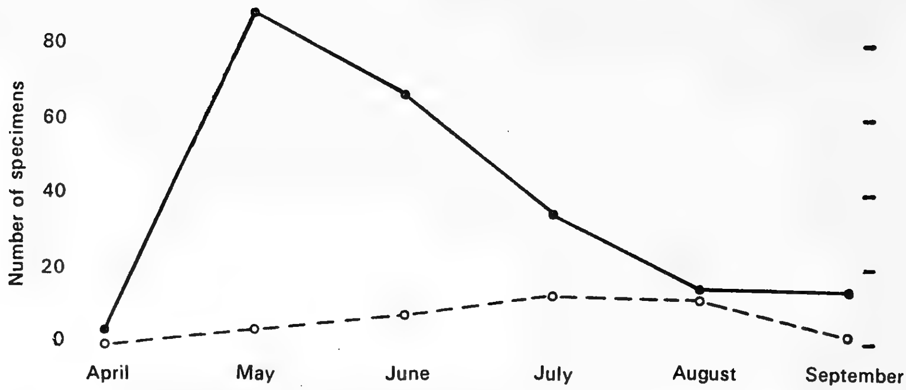


Diagram 54. Number of specimens of Carabidae in Fennoscandia observed spontaneously flying in different months.

(*Bracteon*, *Chrysobracteon* and *Cicindela* not included.) Continuous line = Imago hibernators. Broken line = Larval hibernators.

From the diagram it is clear that the larval hibernators (s.l.) generally fly less: altogether 39 specimens were observed as against 227 among the imago hibernators. The former included a smaller number of species. In the
581 Fennoscandian fauna the ratio of "L species" to "I species" is 1 : 3. Moreover the former comprise comparatively more constantly flightless species (22 as against 27) as well as dimorphic species (16 as against 34). Bearing this in mind we obtain the following figures.

Larval hibernators capable of flight (including dimorphic species): 67 species.

Imago hibernators capable of flight (including dimorphic species): 246 species.

Ratio 1 : 3.7.

Larval hibernators capable of flight (excluding dimorphic species: 51 species.

Imago hibernators capable of flight (excluding dimorphic species): 212 species.

Ratio 1 : 4.2.

However, the observations on flight depicted in Diagram 54 and summarized above give a ratio of 1 : 5.8 between "L species" and "I species."

Even remembering that the "L species" are less well endowed with flight capacity, we conclude that the larval hibernators are less disposed to flight. We are not far from the hypothesis *that the flight of carabids is often associated with the hibernation*.

At any rate, in the carabids there is no question of a "nuptial flight." Nor

is flight in the males for the purpose of seeking the female: the two sexes participate in flight in about equal numbers.* *The flight of carabids is primarily to bring about a rapid, occasionally major change of quarters.*

This change of quarters using flight is in different seasons for the larval and for the imago hibernators. In the former it comes as soon after emergence as they are hardened enough to use their wings, in midsummer, when the biotopes occasionally dry up and become uninhabitable. The larvae could hardly escape with their slow locomotion.

The imago hibernators on the other hand emerge late in the summer half-year and occasionally remain in the pupal stage through the winter. During that season there is seldom any danger of drying up, and the falling temperatures (especially at night) make the flight more difficult. In the next spring, when
582 the insect wakes up, it is usually situated where the larva lived last summer. But in spring the locality may offer very different living conditions, especially with regard to moisture. Less often the imago uses flight to emigrate from a summer biotope markedly inundated in autumn to a drier locality. Hence in the imago hibernators the change in quarters takes place chiefly in *spring*, and Diagram 54 clearly shows that by far the most numerous observations of spontaneous flight were made in May.

During my study of the riparian fauna at Ösby Lake (Upl Djursholm; Lindroth, 1943a) I had the opportunity to study this change of quarters more closely (see also Palmén, 1945). H. Krogerus (1948) developed the same theme to a greater extent after extensive study. It was shown, among other things, that on Ösbysjön the riparian fauna is extraordinarily unstable. In winter, only a few species remain on the extreme edge of the shore; several of them gradually move up to hibernate on drier ground, and finally some cover long distances using their wings. Good examples are the *Chlaenius* species, *Oodes gracilis, Pterostichus aterrimus*, and also some species of *Agonum*, *Bembidion*, etc. In the case of *Oodes gracilis* it was shown that the inclination for flight is strong in spring, but in midsummer vanishes to the extent that the insects cannot be induced to fly by any means. Yet, there can be no question of a reduction in the flight muscles, etc. In autumn the inclination and capacity to fly reappear, not only in freshly emerged specimens but also in ones at least a year old, which showed incapacity for flight in summer.

The significance of flight capacity for riparian species of fresh water margins is therefore quite clear. Darlington (1936, p. 159) correctly emphasizes that the possibility of a rapid change of quarters is not so important for any other ecological group, not only on account of the seasonal changes in shore biotopes, but also because of frequent catastrophes caused by flooding. He points out (p. 160), that the animals of the seashore live under more stable

*In this connection unfortunately no statistical data can be given, since the sex of the flying individuals was not noted in enough of cases.

conditions and are therefore more commonly flightless. Examples of this in our fauna are *Aëpus marinus* and *Trechus fulvus*. The only species bound to fresh water shores that seems to be constantly flightless is *Elaphrus angusticollis*.

Palmén (1944, p. 133) vividly describes how a population of *Bembidion doris* saved itself from the impending drying up of its biotope by flying away.
583 The importance of flight is of course clearer in the case of riparian species than in other ecological groups. But one must not presume some causation different in principle. The best support for assuming that the flight capacity of the carabids serves mainly (at least in imago hibernators) for change of quarters seems to be the dominance of this phenomenon in spring, a season when a change of quarters is most often necessary. For even in biotopes other than shores this season brings about the most extensive and the most sudden changes, especially with the melting of snow.

I cannot judge Palmén's hypothesis (1944, p. 126; cf. Glick, 1939, p. 129) that electrical disturbances in the atmosphere may act as a strong stimulus to flight.

A decisive question from the zoogeographical viewpoint is whether the *direction of flight* of insects is totally accidentally determined. We pass over the fact that the sense organs must produce some movement toward surfaces that suit the insect. It is not known how this happens in carabids. However, it must be assumed that a hygrophilous carabid, for instance, is capable of sensing the proximity of a body of water during flight, bringing about a change of course if need be.

Here we should investigate whether under identical conditions of the earth's surface other factors, so to speak inconsequential for life, can affect the flight direction of carabids. Two factors suggest themselves: *air currents and light*, chiefly that of the sun.

Most carabids are such poor fliers that atmospheric currents—chiefly those directed horizontally, i.e. winds—cannot but affect the direction of flight. Exceptions are the 9 species of *Cicindela, Chrysobracteon* and *Bracteon* mentioned on p. 579 above. Demoll (1918, p. 6) gives the velocity of flight of *Cicindela* (tiger beetle) as 1.8–2.3 m/sec. (The frequency of wing beats in *C. campestris* is 82–87 according to Sotavalta [1947, p. 97].) The others in my experience fly so slowly that they are easily overtaken without running.
584 For *Oodes gracilis*, a comparatively good flier, I measured the velocity of flight with a stopwatch by making the specimens fly indoors (24°C). They always flew to the window 5 m away. I obtained a mean value of 1.6 m/sec from 20 readings (extreme values: 1.25 and 1.85). The variations may be due to deviations from rectilinear flight.

So the flying carabids can be carried along by comparatively weak winds or blown off course. In a very light wind, according to several observations, they mostly *fly against* it.

Interesting results in this field, chiefly with Diptera and Lepidoptera, were

obtained by Lutz (1927), who collected night-flying insects in 8 traps placed in a circle and noted the distribution in them according to the prevailing wind. He established that in a *light* wind the insects fly chiefly against it (cf. also Glick, 1939, p. 114). As he correctly emphasized, this observation does not contradict the fact that flying insects are carried in *the direction of the wind even by a moderate breeze*, whichever way they are headed.

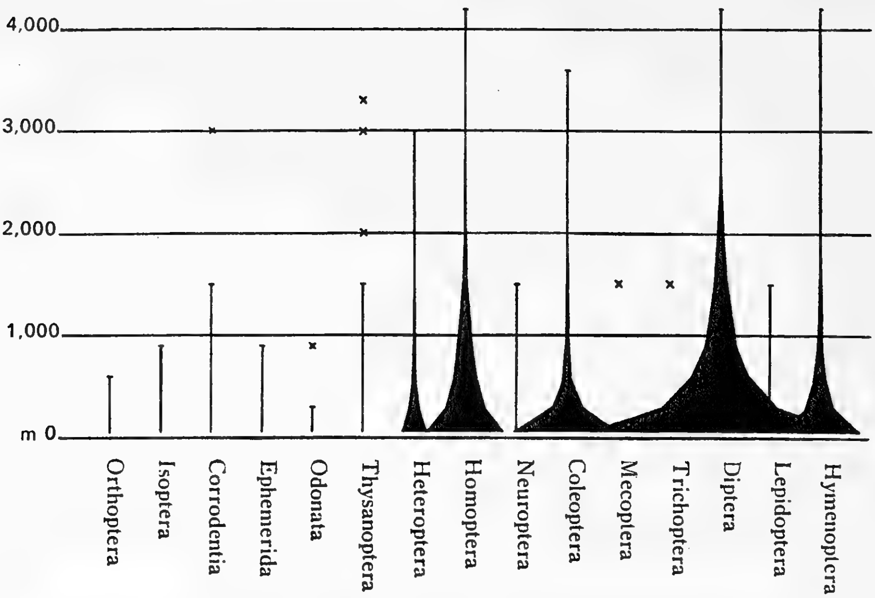
This experiment certainly applies fully to carabids. Since, with the above-mentioned exceptions, they are slow fliers it is clear that change of place even with a light wind is largely determined by it. The insects are more or less passively carried by strong winds. The complete dependence of the anemochorous transport of insects on the direction of the wind has been best elucidated by Palmén (1944, for instance, pp. 194 ff.). Examples of wind transport of carabids were also given above (pp. 282, 287, 295) in connection with the insular faunas. In view of the extensive literature on the transport of insects by wind, reference may also be made to the summaries by Holdhaus (1927–28, pp. 599 ff.) and Uvarov (1931, pp. 116 ff.).

In recent years the subject of the anemochorous transport of animals and plants has been greatly extended by collections from aircraft: it has acquired a firm footing. Wind transport of pollen and cryptogam spores, even over long distances, was already known earlier (for example Bror Pettersson, 1940), but the large component of insects in aeroplankton was a surprise. By far the most extensive collections were made in North America, chiefly to a height
585 of 1500 m (5000 feet). On the basis of the data on catches provided by Glick (1939), three diagrams (Diagrams 55–57) are published here to illustrate the distribution and relative abundance of the insect groups collected at different altitudes.

Among the flying insects (Diagram 55) the Diptera predominate, constituting 40% of the entire material. They are followed by Hemiptera (nearly 17%), the Coleoptera (a good 14%), and the Hymenoptera (11%). The greatest altitude (more than 4000 m) were attained by Hemiptera *(Cicadina)*, Diptera (Tipulidae, Cecidiomyidae) and Hymenoptera.

Division of the collected Coleoptera into the larger families (Diagram 56) shows a substantial dominance of Staphylinidae (39%), which are represented at almost all altitudes up to 3300 m; these are followed by Chrysomelidae (14%), found regularly up to 1500 m, and one *Diabrotica* at 3300 m. The Carabidae occupy third place, which with 470 specimens—including 30 definitely determined different species—comprise a good 13% of the entire beetle
586 material. They were found regularly up to a height of 1800 m; at 2400 m one *Tachys* and at 3000 m one *Microlestes* (*Blechrus*) were collected.

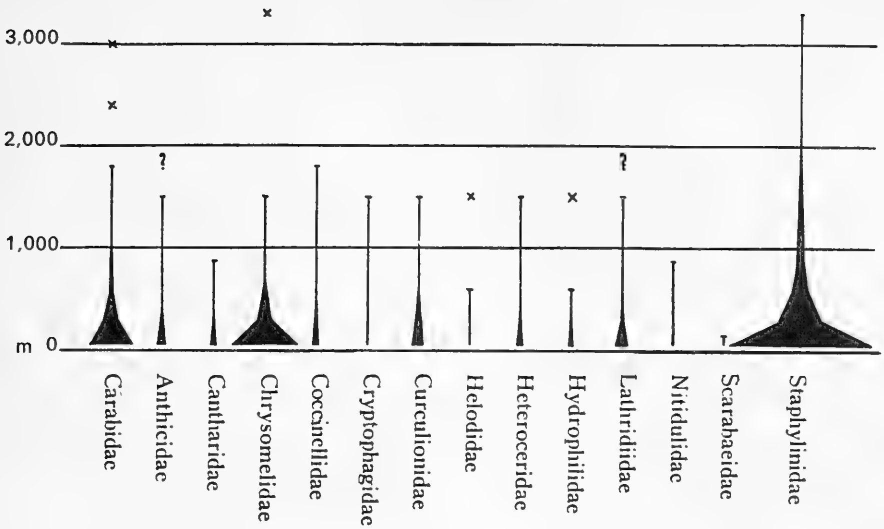
A really big surprise among the results Glick obtained—though foreshadowed by Berland's investigations (for example, 1935, 1937)—is the regular occurrence of *flightless arthropods* in aeroplankton (Diagram 57). With regard to the *araneids*—which do have functional flight capacity—this was expected:



585 Diagram 55. Distribution and relative abundance of flying insects in the atmosphere according to data supplied by Glick (1939). Isolated samples are indicated by crosses.

they even reached the greatest measured altitude of 4500 m. But even *acrids* and wingless insects as well as flightless immature stages of winged species were regularly found at heights of more than 500 m. A *Collembola* (*Bourletiella*) was collected at 3300 m. Of particular interest to us is the fact that a *coleopteran larva* (*Trogoderma*, family Dermestidae) was collected at 2700 m, and that it
587 was *alive*. It was the greatest altitude at which any living animal was found in these collections (Glick, 1939, p. 93).

The impressive documentary material obtained with these American investigations leads to the following conclusion: Most Carabidae (exceptions given on p. 579) are poor fliers and being easily captured by ascending convection currents may be carried into the upper air. Berland (1935, p. 91; 1937, p. 26) notes that only inept fliers let themselves be carried up to great heights.
588 It is obvious that the Lepidoptera and Odonata are less abundant in Glick's material. In higher layers of the air, the velocity of wind is much stronger than near the ground; and above 500 m it is more stable (Ostman, 1933, p. 16; Angström, 1946, p. 86)—even with changing wind conditions close to the ground. At that height (600 m or above) Glick caught 35 specimens of Carabidae. Insects which happen to come in altitudes that high have an unique possibility at their disposal, the *long-distance transport*. The best-known exam-



586 Diagram 56. Distribution and relative abundance of larger families of Coleoptera in the atmosphere, according to data supplied by Glick (1939). Crosses indicate isolated finds, question marks indicate findings made above 1500 m without exact determination of altitude.

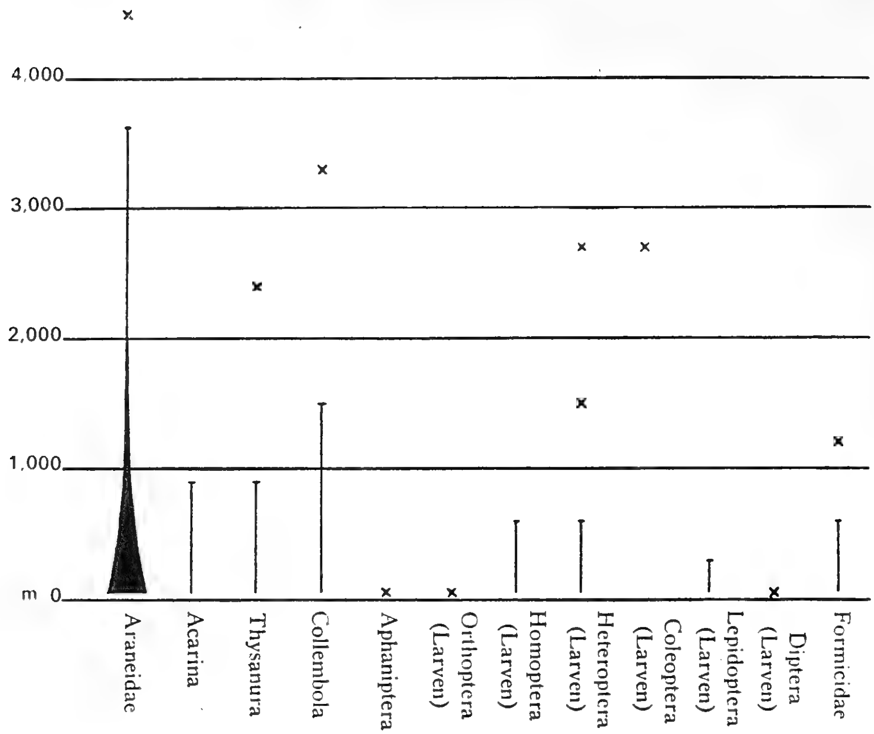
ple to date is that of the occurrence of large numbers of the aphid *Dilachnus piceae* Panz. and of *Syrphus ribesii* L. in the snowfields of northeastern Spitzbergen, where they could have arrived (*Dilachnus* is associated with *Picea*) only by wind transport from over 1300 km away (Elton, 1925, pp. 291 ff.).

Does this transportation in the upper air hold any special importance for the dispersal of Carabidae? In this connection the following facts may be considered:

1. The aeroplankton "population" is extremely light. For the stratum just above the 500 m limit ("2000 feet") Glick calculated the mean volume of air per insect as 877 m^3. Per carabid (corresponding with the component of this family in the fauna above 500 m) this means a good 65,000 m^3, and for the species (*Stenocellus tantillus* Dej.) that was most numerous above 500 m (represented by 4 specimens) it means a good 570,000 m^3 per individual.*

It cannot be denied that such an individual can survive long-distance transport through the upper air—Glick (1939, p. 93) found living coleopteran adults at least at 600—and that it can accidentally land in a suitable region not earlier colonized by the species. But the chance of its landing sufficiently close to an-

*All these calculations are depending on the collecting equipment being 100% efficient, on which I cannot pass judgment.



587 Diagram 57. Distribution and relative abundance of flightless arthropods in the atmosphere according to data supplied by Glick (1939). Isolated samples are indicated by crosses.

other individual of the opposite sex, arriving by the same means, is zero. This kind of colonization becomes a real possibility only if it is shown that even *impregnated females* can stray into the upper air during flight; this question is touched on below (p. 595).

On the other hand—in contrast to the carabids—long-distance dispersal through the upper air can play a role in the expansion of the area of species that show periodic or nonperiodic mass multiplication, such as phytophages, including their parasites and more or less monophagous predators, and also *parthenogenetic* animals.

589 2. The only unambiguous cases of wind transport of insects that have been precisely analyzed, namely insects washed ashore on the north coast of the Gulf of Finland, show such good correspondence with the wind conditions prevailing, during transport, in the air strata close to the ground that the dependence on them seems indubitable (Palmén, 1944, p. 93). At any rate, wind transport at low heights (about < 500 m) and over moderate distances is

the *normal* phenomenon. Moreover, Glick's material (Diagrams 55–57) shows how much richer the fauna of the lowest 300 m is.

3. If long-distance dispersal through the upper air were a normal phenomenon and regularly led to colonization, then—in my opinion—the distribution of some carabid species would have definitely been different. Foremost the area displacements, for instance the post-glacial immigration into Fennoscandia, would have involved erratic advances rather than a gradual shift. A species like *Amara majuscula*, which on account of its pronounced inclination to flight has produced true swarming flights in Poland, and is especially suited for anemochorous transport, certainly would not have had such regular immigration into Fennoscandia as indicated by the map in Fig. 84 (p. 625) if this represented the consequence of long-distance dispersal in the upper air.

The only species whose occurrence in Fennoscandia one might be inclined to ascribe to such transport would be *Lionychus quadrillum* for its isolated locality near Nke Örebro. However, here transport by man seems equally probable.

The answer to the question raised above is therefore: *long-distance transport in the upper air, as a mode of dispersal for carabids, plays at the most a minor role.* On the other hand winds close to the ground and the speed of flight are of decisive importance. Favorable winds are not only responsible for the insects washed ashore along the Gulf of Finland, but without them *Amara majuscula*, as well as those immigrants discussed above (pp. 282, 287, 291), probably emigrating from the eastern Baltic, in the fauna of Gotska-Sandön, Fårön, and Gotland, could not have covered the much longer aerial route. Hence the Baltic Sea is not an effective barrier against the dispersal of flying forms, which is illustrated below (p. 610) with further examples.

590 It is interesting—but basically to be expected—that *a good active flight capacity*, which among carabids is possessed only by *Cicindela*, *Bracteon*, and *Chrysobracteon*, actually *diminishes the dispersal capacity* (similar findings were made by Ekman, 1922, pp. 333–334, by comparing the dispersal tendencies of mammals and birds). This can be explained by the fact that these animals are only rarely transported passively (by especially strong winds). The result is that they often show an inexplicable conservative attachment to small sections of biotopes that do not perceptibly differ from the surroundings—at any rate when viewed with human eyes. Such an observation is made by Krogerus (1932, p. 238) with regard to *Cicindela maritima* near Nl Tvärminne, and Horion (1937, p. 9) reports two localities of *Bembidion litorale* (which is otherwise stenotopic, bound to river-banks) on a standing body of fresh water. It turned out to be a cut-off old river course so that these were probably relict occurrences. Moreover, the Fennoscandian area of these two species, and that of *Bembidion argenteolum*, as a whole has a markedly "conservative" imprint. An exception is provided by the two apparently accidental records of *Bembidion* (*Bracteon*) *striatum* near Nl Tvärminne and in Møen in Denmark.

Starting from Glick's material it is necessary to take up another, very important question: *Is it conceivable—whatever the height above ground—that flightless carabids or immature stages of carabids can be transported by the wind?*

Even apart from the Araneida, which are functionally capable of flight suspended from their threads, remarkably many-wingless animals have been found in aerial plankton collections (Diagram 57). Glick's numerical data (1939) are given below:

Acarina	44 specimens
Thysanura	40 specimens
Collembola	26 specimens
Aphaniptera	1 specimen
Formicidae	20 specimens
Orthoptera larva	1 specimen
Hemiptera larvae	29 specimens
Coleoptera larva	1 specimen
Lepidoptera larvae	5 specimens
Diptera larva	1 specimen.

This shows that these animals belong to any one (possibly two or more) of the categories below:

591 1. Very small animals, for example, Acarina, Collembola.

2. Weakly chitinized—hence "light"—animals, for example, immature Hemiptera.

3. Animals with dense pubescence or other appendages, for example, Thysanura, *Trogoderma* larva (Coleoptera).

4. Animals that spin threads, for example, Lepidoptera larvae, of which 3 were found to belong to the family Gelechiidae.

5. Animals that live in the open and visit the upper parts of the vegetation, for example, workers of Formicidae.

Adult carabids can only exceptionally be considered in categories 1 and 5. Undoubtedly they are safe from being captured and carried up by convection currents chiefly because of their marked chitinization—and their "weight" (which can be appreciable in brachypterous species). The earlier stages of carabids, especially eggs and pupae, all inhabit very concealed habitats. The larvae have no appendages (the cerci are rather short and weakly developed) nor any pronounced pubescence that could catch the wind. It is significant that the only coleopteran larva in Glick's material belongs to the family Dermestidae, in which the larvae are characterized by very dense pubescence, arranged in tufts. These theoretical considerations support the view that little significance need be attached to wind transport of flightless carabid adults or of their immature stages.

However, there are also facts to prove it. The clearest are provided by maps of the distribution of macropterous and brachypterous forms of some

dimorphic species. We found earlier that the area of a dimorphic species in process of dispersal is characterized by the presence of a more or less broad "belt" of purely macropterous populations at the area limit. Good examples are *Calathus mollis* (Fig. 28, p. 368), *C. erratus* (Fig. 35, p. 376), *Bembidion aeneum* (Fig. 49, p. 400), and *B. grapei* (Fig. 50, p. 402). This fact is comprehensible *only if regular dispersal through the air involves only carabids capable of flight.*

In Fennoscandia there is no record of a flightless carabid so isolated and unexpected as to suggest long-distance wind transport.

On the other hand Gislén (1940, pp. 19 ff.), for instance, rightly attaches
592 great importance to the dispersal of flightless "very small animals" as aeroplankton. But besides the advantages (also emphasized by Gislén in a later contribution, 1948, p. 121) of the small weight of these animals and their tenacity in the encysted condition (l.c., p. 21) many of them can reproduce asexually (for example, in Protozoa and Rotifera).

In *conclusion* it may be stated, with regard to the wind transport of carabids, *that it may involve only imagines, and of these only individuals capable of flight.* At any rate, other cases seem to be so rare that they are inconsequential for the expansion of area. However, for carabids capable of flight, wind transport has a decisive role, both by extending the distance covered and by determining the direction of the flight. There is no evidence of the effect of long-distance transport in the higher layers of the air.

The second factor that can affect the direction of flight of an insect is the *light*. It is an age-old observation that many night-flying insects, including carabids, are attracted to artificial light. But so far no one has remarked that "natural" light, the *sun*, could have a similar effect.

Two observations led me to these considerations:

First, the conditions on many islands of the Baltic Sea, chiefly on Åland and Gotland, including the small neighboring islands. It is clear that the flying element of the carabid fauna of these islands has come more from the east than from the west, even though the prevailing winds—especially in the case of Åland—might favor migration from the west (pp. 254 ff.).

Second, the fact that 4 (possibly 5) species in Sweden each have an isolated locality in the Bothnian coastal region far north of the continuous area, which extends much farther north in Finland. See Table on p. 520.

Hence these isolated localities are much more closely related to the Finnish than to the Swedish area, which is hard to explain except by migration across the Bothnian Sea from the east. All these species are demonstrably capable of flight. The explanation is confirmed in the case of *Anisodactylus* by the finding
593 of this species on the tiny island of Oa Norrskär in Kvarken. It is interesting that we know of no species that colonized a new area by flying in the opposite direction across the Bothnian Sea—from Sweden to Finland. And the winds are of course favorable for such transport, even in the higher layers of the air

	Isolated locality	Elsewhere in Sweden or northward as far as	In Finland northward as far as
Acupalpus dorsalis	Vbt Vännäs 63° 55	Hls 61° 15	Om 64° 7
Anisodactylus binotatus	Ång Örnsköldsvik 63° 15	Hls 61° 48	Om 64° 50
Asaphidion flavipes	Ång Örnsköldsvik 63° 15	Gst 60° 20[1]	Oa 62° 50
Chlaenius tristis	Mdp Alnön 62° 25	Upl 60° 7	St 61° 30
Oodes helopioides	Mdp Timrå 62° 28	Gst 60° 45	Oa 62° 58[1]

[1]In the Swedish inland (Dlr) *Asaphidion flavipes* was found as far as 61° 42′, in eastern Finland as far as 61° 20′. *Oodes helopioides* was also found farther north in eastern Finland.

(Östman, 1933, p. 30).

The following conclusion is obvious: The flight direction of these species is affected by some factor independent of the wind conditions.

To test how far the sun might be such a factor, I performed the experiments mentioned above (p. 256) in a special "flight direction apparatus" (Experiment 147 ff., p. 109). It was found that the 6 species tested—with the exception of *Badister peltatus* (for which inadequate material was available)—show a distinct inclination to fly toward the sun. It is interesting that *Acupalpus dorsalis* is one of the species we mentioned above as an example of a species that arrived in Sweden from Finland across the Bothnian Sea.

Especially decisive for the orienting effect of the sun on the flight of an insect species responding positively to it, is the daily time of flight. It is to be assumed that the closer the sun is to the horizon, the greater its effect; hence insects that fly at the time of sunrise or sunset should be particularly affected. In addition to light, a sufficiently high *temperature* is a key factor for flight activity; the flight of carabids is closely dependent on it (see, for instance, McClure, 1943, p. 38). It can therefore be argued that for species
594 that—exclusively or predominantly—fly in weak daylight the morning hours are rarely warm enough, so they become more or less regular *evening fliers* (McClure, l.c.).* For the same reason the nocturnal insects fly chiefly in the first half of the night when, for an hour or so, the afterglow is still effective. Accordingly, the flight direction of the species that fly during the hottest mid-day hours should be determined least of all by the sun. Carabids are chiefly evening fliers—the above mentioned *Acupalpus dorsalis* included, of which mass flight was observed in the evening (Palmén, 1946, p. 32). A considerable

*McClure made systematic collections (morning and evening) of flying insects in Kentucky. In his material the carabids were represented by 88 specimens belonging to 20 species, of which 4 were collected in the morning and 84 in the evening.

number of carabids fly exclusively at night and can be collected in a light trap. Further information is given against each species in Part I of this contribution.

If the carabids use their wings chiefly in the evening or during the first hours of the night, it follows that, to the extent that they generally respond positively to the sun, they *tend to fly west.*

In this way it appears to me that a plausible explanation is provided for the two above-mentioned observations with regard to the flying element on certain Baltic Sea islands and on either side of the Bothnian Sea. It would also be worth testing other species in the "flight direction apparatus," for example *Amara majuscula*, whose unprecedentedly rapid immigration, apparently emanating from the southeast, is discussed later (p. 622), and *Bembidion transparens*, whose macropterous stock in the south Baltic region is unmistakably of eastern origin.

The general effect of the "sun rule," not only on carabids but on insects generally, cannot be decided in the present state of our knowledge. First of all it must be established for every species of insect whether it responds positively to the sun and what time of day it usually flies (with regard to night-flying Lepidoptera, in this connection, see Williams, 1939, pp. 119 ff. ; Ellinor Bro Larsen, 1943). It must be pointed out that the two clearest examples of Lepidoptera that have immigrated recently from the east, *Phytometra confusa* Steph. (Nordstrom, 1945) and *Eupithecia sinuosaria* Ev. (Wahlgren, 1921)*, are night-flying insects, whereas generally well-known immigrants (some of which are only transgrading species) which, as far as is known have arrived from the south, such as *Colias hyale* L., *C. electo* L., *Pyrameis atalanta* L., *P. cardui* L., and *Phytometra gamma* L., and are *diurnal insects***.

If, as I expect, it turns out that the sun *affects* the flight direction of a large number of flying insects, this will probably also throw light on the important role played by *the Siberian fauna* in the post-glacial recolonization of northern and southwestern Europe. Perhaps it will even be possible to show that at high latitudes (i.e. above the Arctic Circle) insect flight is somewhat deflected toward the pole, on account of the summer position of the sun, but near the Equator is more strictly inclined toward the west.

The significance of flight capacity and of wind transport for the dispersal of a species of insect can be correctly estimated only if it is established *whether impregnated females fly or not.**** It is clear that if they do, the possibility of permanent colonization of a new region is greatly enhanced.

*I cannot agree with Wahlgren's view (1912, p. 161), that the rapid dispersal of *Eupithecia sinuosaria* westward is chiefly due to transport by man.

**It must also be investigated whether the direction of migration of the transgrading sphingids (*Acherontia,* etc.) is governed by particular factors.

***In parthenogenetic species, which, as far as is known, do not occur in the family Carabidae, this question does not arise.

Experimentally this could be tested by two methods: On the one side by isolating females found flying in nature, to establish the possibility of laying fertilized eggs; on the other side by inducing females after observed copulation to fly, later ascertaining whether they were actually impregnated.

I have tried both methods, but unfortunately with very little material and only moderate success. Females of the following species caught during flight were isolated: *Amara aenea* (caught on May 13), *Amara familiaris* (3 specimens : May 6, May 13, May 13), *A. ovata* (May 23), *A. similata* (May), *Bembidion rupestre* (May 13), *Harpalus distinguendus* (3 specimens, May 13).
596 Oviposition could not be established in any of these cases.

I tried the other approach with *Oodes gracilis*. Five pairs of this species were kept separately (May–June 1945) in glass dishes. Copulation was observed only in one case, but had probably taken place in all cases. After a few days the females were compelled to fly using strong artificial light, which succeeded in all cases, after which each of them was isolated in its glass dish. In two of them a very small larva was discovered in each after 11 and 13 days respectively, and another after 16 and 19 days respectively. *So these two females flew with fertilized eggs*.

It was thus shown that impregnated females *can* fly at least in certain cases; it is another matter whether they can do so in nature. As discussed above (p. 581), the flight of carabids in most cases (especially in imago hibernators) serves to change the quarter. Meeting of the sexes and copulation may take place, with few exceptions, only at the summer abode, after the obligatory flight. Thereafter the next occasion for flight is normally only in autumn—assuming the adults, which have already overwintered once, survive. There are exceptions: hygrophilous insects living on very small, particularly standing bodies of water can be threatened in summer with desiccation and compelled to escape through the air (p. 582). In line with this, we cannot ignore the possibility that two dimorphic riparian species (*Bembidion assimile* and *B. transparens*, p. 395) have been able to spread in the brachypterous form by means of the flight of impregnated macropterous females. On the other hand this does not seem to happen in the case of the chiefly ripicolous *Bembidion aeneum* (Fig. 49, p. 400), nor in the case of *B. grapei* (Fig. 50, p. 402), *Calathus erratus* (Fig. 35, p. 376) or *C. mollis* (Fig. 28, p. 368), since these species have a "purely" macropterous stock at the periphery of their area.

I believe that the flight of impregnated females in Carabidae is a rather rare exception. But this important question must be investigated carefully with more material, preferably the anemohydrochorously transported insects common on the Finnish south coast (p. 604; Palmén, 1944). For this purpose
597 females still swimming on the water, which have not yet found males, should be isolated to determine to what extent they are impregnated. I believe it will be found that they are not. This is supported by the fact that so many species repeatedly found in this drift material have failed to colonize the new

region permanently (indicated by an asterisk in Palmén, 1944, pp. 37 ff.). Of these, among the carabids at least for *Acupalpus flavicollis*, *Bembidion assimile* and *B. illigeri* the necessary climatic and other existence requirements in southwest Finland can hardly be lacking (see maps in Part II). Of course the first-mentioned species (according to a personal communication from Palmén) now (since 1946) seems to have actually become resident in the Tvärminne region.

The following conclusions can be drawn on the dynamical significance of flight and of wind transport for carabids:

1. The few good fliers (*Cicindela,* 5 species of *Bembidion*) are not transported over long distances. They are strikingly "conservative" and show slow dispersal.

2. The other forms capable of flight are largely influenced by the wind and can be transported with it over long distances, for example across the Baltic Sea.

3. Transport in higher layers of the air (> 500 m) has at the most minor significance.

4. The direction of flight is also affected by the sun, such that insects flying in the evening and at the beginning of the night—moving toward the sun—have an inclination to fly *west.*

5. The area-expanding effect of flight and of wind transport is minimized by the fact that impregnated females rarely fly. However, this problem is offset in the case of anemohydrochorous transport (p. 604), where—on account of the large congregation of individuals in the new region—a meeting of the sexes *after* transport is facilitated.

6. Despite these important reservations it is clear that carabids capable of flight, are benefited in dynamics in contrast with the flightless carabids. It appears that passive wind transport of the latter can be discounted.

The principal difference in the dispersal capacity of species capable of flight and of flightless species, however, is not so clear in Fennoscandia: the
598 devastation of the Quaternary glaciations permitted, with few exceptions, the survival or postglacial immigration of only such completely soil-bound insect species as are markedly *eurytopic.* Because of this these species also have a great advantage in dynamics, which can give them a strong advantage over species capable of flight but markedly *stenotopic.*

On the other hand, in the central European mountains, chiefly the Alps, where the possibilities of glacial hibernation were far greater, the sharp difference between insects capable of flight and flightless insects regarding the size of the area—i.e. the capability of dispersal—is clearly evident, not least among the carabids. Many non-flying species have very small terrains of habitation, sometimes a single mountain peak. Examples of such carabids, also from other regions, are given by Holdhaus (1927–28, pp. 597 ff.) and by Heberdey (1933).

Water Dispersal

The range of transport of insects by water is a function of the water's movement and the ability of the animals to survive a sojourn.

Experiments on exposure to water—some of them with carabids—have been conducted by numerous researchers, particularly by the following on Nordic beetle material: Mjöberg (1912, pp. 198–199), Lindroth (1931, pp. 484–485), Krogerus (1932, p. 237), Frey (1937, pp. 430–432), Palmén (1944, pp. 154 ff., 1945, p. 29), Backlund (1944, 1945, pp. 140–141). My experiments with the species of *Cymindis* are described in the present contribution (p. 248).

These studies showed that most beetles readily tolerate exposure to water for more than one day. Survival is longest in species that are able to float on the surface (Lindroth, Frey), for example, *Cercyon litoralis* Gyll.: up to 22 days (Backlund). In this respect the carabids are favored by their large elytra, which are closely juxtaposed and can retain a considerable quantity of air in the subelytral space where the stigmata openings are located (Lindroth and Palmén, 1944). But *Dyschirius obscurus,* for instance, can even endure complete submersion for 7–8 days (Krogerus) (in winter much longer: see below). This is important, since in nature, especially with rapid water transport in rivers
599 and waves, insects are incessantly splashed by the water when not transported on drifting objects.

Some insects—including terrestrial forms—can perform active swimming movements on the surface of water. They are better suited than others to struggle toward a nearby bank, more or less independently of the movement of the water. The carabids are favored in this respect (Joy, 1910, p. 383). In *Agonum marginatum*, Palmén (1944, p. 78) recorded a swimming speed of up to 4 m per minute (water temperature 18–19°C). In *Broscus cephalotes,* I obtained a corresponding figure of a good 2 m (water temperature 15°C) and a mean value (from 9 observations) of 1.8 m. According to Joy (l.c.), *Agonum ruficorne* even has the ability, like *Dianous* and certain species of *Stenus*, to secrete a fluid from the abdominal tip which drives the insect forward.

Since I assumed *Broscus cephalotes* to be a flightless species (p. 574) it was interesting to study its resistance to exposure to water (Experiment 146, p. 109). Four specimens were studied, two of which were left swimming undisturbed on the surface of the water, whereas the other two were vigorously shaken 3 times daily. The room temperature was high (> 20°C).

Length of life of 2 specimens undisturbed: 9 3/4 and 11 1/2 days, respectively.
Length of life of 2 specimens shaken up in water: 9 3/4 and 17 1/6 days, respectively.

Considering the high temperature during the experiment, *Broscus* must be considered markedly resistant to exposure to water. A big advantage in nature is its indifference to being splashed with water (cf. the species of *Cymindis*,

p. 248). This is certainly due primarily to the firm attachment of the elytra along the suture (p. 575), so that a quantity of air essential for respiration can be retained in the subelytral cavity. Hence *Broscus* is an insect with a good possibility for surviving long-distance transport by water even without the protection of drifting objects. To explain its occurrence on Gotska Sandön in this way (p. 285) may not be too bold.

Three "external" factors particularly affect the ability of insects to tolerate exposure to water: First the *temperature*; a low temperature prolongs *survival in water*, especially in carabids (Palmén, 1944, p. 169; 1945). It follows that transport by water is easier in the winter half-year, i.e. the imago hibernators are favored in this respect (p. 205).

600 Second, the *salt content* of the water. Palmén (1944, p. 155) conducted instructive experiments which clearly show that the high saline content of the open sea (> 30 per mille) has a harmful effect on most insects. It causes physiological desiccation of the animal, which more or less sharply shortens its life. Baltic Sea water (< 10 per mille) seems not to have such detrimental effect. These experimental results were clearly confirmed by zoogeographical findings. In particular, the fauna of the North Sea islands considered earlier (p. 325) shows, that colonization by hydrochorously transported flightless species has taken place chiefly in winter (in part probably with ice), and that it has been more effective at the mouth of the larger rivers. On the other hand in the Baltic Sea, Gotska Sandön, for instance, evidently obtained the corresponding element to a great extent by purely hydrochorous transport during the summer half-year.

Third, the occurrence of all kinds of drifting *solid objects* in water has a very important role in the possibility of insects to survive long-distance transport. We found above (p. 248) that *Cymindis macularis,* which has colonized certain Baltic Sea islands probably by hydrochorous transport in summer, has such poor resistance to exposure to water, that long-distance transport might be conceivable only with the help of floating plant material and the like. This species lives chiefly on sandy banks in the immediate vicinity of the sea. It is therefore quite conceivable that some individuals may be set adrift, for instance, by a strong stormytide, along with a fascicle of *Psamma* or *Elymus.* In these fascicles even with constant splashing by the waves, there are sufficient air spaces, chiefly under the leaf sheaths, for a safe journey. The same kind of transport may be assumed with still greater certainty for the colonization by *Dromius linearis* of the Swedish east coast and the Skärgård of Åland, where this species is often found on very small skerries. It lives here normally in fascicles of grass, always in the brachypterous form.

The most important "object" offering hydrochorous transport is the *ice*, and there are several reasons for assuming this. First of all, as already mentioned, the low temperature itself increases the resistance of the insects. Second, the insects on the surface of ice-floes can remain as good as dry,

especially when it carries reeds, straw and the like. When such parts of plants, for instance, stems of *Phragmites*, are present in the solid ice, the insects
601 can survive for months *frozen in the ice* (Palmén, 1945, p. 32). Moreover, with a sufficiently strong wind, drift ice can move fairly independently of the ocean currents. Ice-floes that enter the sea through river mouths with spring floods are especially advantageous. They are more likely to have been covered with soil, plant parts, etc., and many also harbor other than purely seashore inhabitants and transport them out to sea. Besides, river ice is especially suited for transporting insects sensitive to saline content, even to islands surrounded by highly saline seawater. For colonization by water transport, of all the islands considered, *Hailuoto* in the mouth of the Ule River is most favored (p. 236); Glomma might have similar significance for the Hvaler islands (p. 318).

It may therefore be justified, in our climatic conditions, virtually to equate hydrochorous transport of insects with *ice transport*. Several concrete examples were given in the chapter on Insular Faunas.

We must now inquire which kinds of movement of water bring about long-distance transport of animals within a reasonable period of time.

The most effective are *rivers*. Their importance in promoting the dispersal of insects of course lies not so much in the insects being washed out to sea (or into lakes), but in that—chiefly during flooding (see, Palm, 1945)—species living on the upper course of a river are passively transported down with the water (see also Holdhaus, 1927–28, pp. 603–604). Especially useful modes of transport are provided by very large vegetation-covered clumps of earth, which often fall into the river on account of the erosion caused by water and are carried downstream (Heinze, 1914). In line with this, both along the northern Swedish rivers (Lindroth and Palm, 1934, p. 123) and near the Klarälven River in Värmland (Palm and Lindroth, 1936, p. 39), numerous accidental occurrences of northern or otherwise cold-loving Coleoptera were observed. In the fjelds it is noticed by those with botanical interests that even high alpine plants of the banks of torrential streams in the *Regio betulina* are carried downstream. In the same way often even *Nebria nivalis* is carried to lower altitudes by rivulets of melted snow from its true home on the edge of the perennial snowdrifts.

602 Whether such river transport leads to permanent colonization and area expansion depends on how far the transported animals can survive in lower locations. For species restricted to the *Regio alpina* and the high altitude forests of the fields, this mode of dispersal has little significance because of their special requirements of cold.

The situation is very different for species of the plains, for which a mountainous region, such as the Scandinavian chain of fjelds, presents a barrier to dispersal. An excellent example of an animal that was able to overcome this barrier—moving from west to east—partly with the help of rivers, is *Bembidion virens*, which I have discussed in this connection (Lindroth, 1935a, p. 624). It

is also possible that the emigration of *Agonum piceum and Pterostichus minor* from Sweden to the Trondheim region is materially assisted by rivers.

An attractive task would be to study experimentally the area-expanding effect of rivers. The task could best be undertaken by "introducing" in sufficient numbers, for instance, along the middle course of the Klar River, a carabid from the temperate parts of North America* which is unpretentious in all respects but is associated with the waterside. In subsequent years regular and precise inventories of the riverside above and below this point should be undertaken. Selection of a large, easily recognizable species would be preferable. Objections to this deliberate "adulteration" of the endemic fauna would probably be raised in various quarters. However, for the reasons given above (p. 555) I do not believe that the introduction of a polyphagous carabid can disturb "the balance of nature," and the purely scientific advantage might be enough to justify the procedure.

In standing water and in the sea, transport is determined partly by *water currents* and partly by *waves* caused by the wind (in the case of drifting objects sticking out of the water, directly by the wind as well). At present most zoogeographers are rightly skeptical of the possibility of long-distance transport of
603 terrestrial animals in seawater (for example, Holdhaus, 1927–28, pp. 625 ff.). In the Baltic Sea the conditions are more favorable on account of the comparatively short distances and the low salt content of the water (p. 518). Botanists especially have cited the "Baltic drift" for the dispersal of plant diaspores (Sernander, 1901; Eklund, 1931). But it is obvious that living animals are much more susceptible to submersion. Hence transport over such a long distance as from the eastern Baltic or Gotland to Åland has been seriously assumed (p. 248) only for one coleopteran species, *Drilus concolor*, the female of which lives in the shells of snails. For other cases where hydrochorous transport to various Baltic islands was surmised, reference is made to the chapter on Insular Faunas. There is also a possibility that *Carabus clathratus* has succeeded in hydrochorously crossing the narrow strait of Kvarken in the Bothnian Sea (p. 381).

The question whether insects are able to cross the Gulf of Finland by purely hydrochorous transport, especially from Estonia to southwestern Finland, has been repeatedly discussed. Frey (1937, pp. 423 ff.) surmises that at least part of the drift material he examined from the region of Nl Tvärminne arrived by this means, but this is justly contested by Palmén (1944, pp. 81–82). Krogerus (1932, p. 238) thinks such transport with drift ice is conceivable, especially in spring. At least in two cases, *Carabus cancellatus* and *C. convexus* (both consistently brachypterous), this assumption seems justified. Both have an isolated occurrence on the mainland in the extreme southwest of Finland. The gap east of it includes the region of Helsinki—the best-explored part of

*If an Asiatic species were selected there would be an outside chance of the same species later reaching Fennoscandia "in the natural way."

all Finland—so it is out of the question that it is due to insufficient exploration. For the same reason it seems inconceivable that the species have been introduced anthropochorously into southwestern Finland, since in that case Helsinki would hardly have been bypassed. The map of *C. cancellatus* shows that the above-mentioned gap cannot be due to climate. *C. convexus* was also found on an island in the Skärgård of Åland, and this was considered (p. 261) the result of hydrochorous transport (possibly with drift ice). It is not too bold to attribute the occurrence of these two species of *Carabus* in southwestern
604 Finland entirely to hydrochorous transport from Estonia across the mouth of the Gulf of Finland (concerning the direction of the sea currents in this region, see maps in Fig. 19, p. 247).

There may not be any further case where hydrochorous immigration to Fennoscandia has to be assumed.

The greatest *effect* of a factor supporting dispersal is attained by hydrochorous transport if it operates together with anemochorous transport—or more correctly after the latter, i.e. as *anemohydrochorous dispersal.* Its importance was correctly appreciated only with Palmén's investigation (1944).

The special significance of anemohydrochorous transport and its superiority to purely anemochorous transport or purely hydrochorous transport lies in the fact that *a long-distance transport over large surfaces is possible without the otherwise inevitable scattering of individuals.* The initial phase, i.e. flight and anemochorous transport, determines the distance and the direction of the journey, and the final phase, the washing ashore, provides for a meeting of the sexes in the new region.

So it can be argued that for a majority of insects cabable of flight —especially among the Coleoptera and Hemiptera—anemohydrochorous transport represents *the most effective passive means of dispersal*, which can lead to permanent colonization. Palmén (1944, pp. 206 ff.) is certainly correct when he stresses the effect of a "Baltic direction of immigration" across the Gulf of Finland, for the coleopteran fauna of Finland. Among the carabids he believes to have immigrated in this way, *Demetrias monostigma*, which, as far as is known, is always apterous in northern Europe, must be excluded (cf. p. 605), and the transgrading *Chlaenius sulcicollis* has no permanent area in Fennoscandia. On the other hand some species can be added. Among carabids that have reached Finland (at least partly) by the "Baltic route of immigration" using anemohydrochorous transport, mention may be made of the following:

Acupalpus consputus
Agonum marginatum
Amara spreta
Bembidion assimile
B. biguttatum
B. schüppeli
B. varium
Calathus ambiguus
Calosoma inquisitor.

605 To a large extent the Baltic islands have also received the flying elements of their fauna in this way, which is evident from the discussion in the section on Insular Faunas (pp. 236 ff.).

It is much more difficult to decide whether the fauna of the Scandinavian mainland has also received a substantial influx by direct anemohydrochorous transport across the Baltic Sea and the Bothnian Sea. Certainly *Dyschirius neresheimeri* arrived in this way. The question was touched on elsewhere (p. 719), but must be left in the main to future investigations.

Transport by Animals

No carabid in the adult stage leads a parasitic existence, and in cases where the larvae are ectoparasitic on other insects—in our fauna at the most in the case of *Brachynus* (p. 548) and *Lebia* (p. 550)—the host (as far as is known) is in an immobile stage (pupa or the last instar larva) and hence cannot actively contribute toward dispersal of the parasite.

Actually as well as theoretically only vertebrates can be considered as accidental transporters of carabids (including their developmental stages). Some authors have made particular mention of *birds*, which can cover long distances in a short time and so can have a role in the colonization especially of isolated islands by all sorts of small animals. In respect of Iceland, I have already (1931, pp. 531 ff.) considered this question in fair detail and concluded that transport of fresh-water animals (for example molluscs) on the feet of natatorial birds may not be altogether rare (concerning the dispersal of aquatic plants by birds, see Samuelsson, 1934, pp. 187 ff.), whereas the "atmospheric animals" have little prospect of utilizing such transport. With regard to insects—aside from bird parasites—mostly the immobile stages alone, chiefly the eggs, are involved, and the possibility of permanent colonization of a new region seems realizable at the most in parthenogenetic species.

Among the Fennoscandian carabids the possibility of transport by birds perhaps rates consideration in a single case, *Demetrias monostigma*. Two facts
606 may be cited: First, the quite isolated northernmost occurrences both on Öland and Gotland, as also in Vrm Visnum and in the region of Helsinki on banks rich in vegetation and in birds. Second, on account of the broad fourth segment of all tarsi in this genus, which is provided with strong adhesive hairs that help the insect climb around on grass stems, etc. and hold on, even against strong wind at exposed places.

Transport by Man

There are very few carabids in the Fennoscandian fauna completely and directly dependent on man. Only two cases are very clear: *Pristonychus terricola* and *Sphodrus leucophthalmus*, both of which are found in our region only in

houses (although one specimen of *Pristonychus* was collected at the entrance of a cave in Gtl Lilla-Karlsö). Ecologically related is *Clivina collaris*, which in our region occurs more or less accidentally in garden soil or even in glasshouses. All three undoubtedly reached Fennoscandia by human traffic.

There are other species not markedly synanthropous elsewhere in their area whose arrival in Fennoscandia is evidently due to transport by man: they occur exclusively in or near cities in strikingly accidental localities. These are *Carabus auratus*, *Pterostichus madidus*, probably also *Carabus monilis*, and possibly *Lionychus quadrillum* (cf. p. 622).

For reasons mentioned elsewhere (p. 632) it is also highly probable that *Carabus nemoralis* and *Dichirotrichus rufithorax*, which are benefited by culture, originally arrived along with human beings.

With the present (in peacetime!) brisk traffic between most European countries it is strange that apparent cases of insects accidentally introduced by man are not more common. Shipments of potatoes, fruits, and vegetables from southern Europe, of onions from Holland, etc. should provide excellent opportunities. In other coleopteran families there are examples of species that have been transported to Europe—including Fennoscandia—from afar areas, even from the Southern Hemisphere (p. 638), although not among the Fennoscandian carabids.

In general the importance of human traffic for the long-distance transport of other clearly synanthropous insects has in my opinion sometimes been
607 overestimated. With regard to Iceland which, on account of the constant import of foodstuffs, timber for construction, etc. must be considered unusually suitable for this purpose, I have (Lindroth, 1931, pp. 506 ff.) argued the contrary in detail. The possibility of an important role for the dispersal of non-synanthropous insects by human beings to this island is contradicted chiefly by the following fact: Iceland and the Faeroes have had identical trade connections from olden times (the same goods are imported from and exported to the same countries). Yet the synanthropous fauna (with clear examples in the genus *Cryptophagus* and among the Collembola) is largely different in the two insular regions, whereas the non-synanthropous species are remarkably identical. "Whoever is inclined to consider the coleopteran faunas of Iceland and the Faeroes as predominantly imported must argue that distribution [better: dispersal] with cultivation mainly affects species not bound to cultivation!"

The faunal exchange between Europe and North America in the historical past with the help of human beings may also be recalled. There are first of all numerous species earlier known from Europe which are believed to have been introduced into America. This undoubtedly holds in the cases of *Pristonychus complanatus* Dej. and *P. terricola*, and certainly also for species like *Carabus nemoralis*. But this kind of interpretation is easily carried too far; for instance, I would no longer assent to the view expressed by Holdhaus and myself (1939, pp. 224, 234) that *Barynotus squamosus* Germ. was introduced

to North America. How small a role such traffic has played in the opposite direction is striking; Holdhaus (1927–28, pp. 612–613) is aware of only two cases (*Stenopelmus rufinasus* Gyll., *Neoclytus erythrocephalus* Ol.), in which true acclimatization of a North American coleopteran species has taken place in Europe, to which unfortunately the Colorado potato beetle (*Leptinotarsa decemlineata* Say) must now be added. Of course, just now there are at least as good possibilities for transport eastward as westward across the North Atlantic Ocean.

But notably opposing the assumption of frequent long-distance transport is the fact that not a single non-synanthropous carabid species has found its way from the Southern Hemisphere into Europe with human traffic. It cannot
608 be seriously denied that numerous species of the temperate parts of South America and Australia (including New Zealand) would be capable of living in the corresponding parts of Europe.

Evidently the possibilities of transport are greater over short distances, for example within the limits of Fennoscandia. It is not impossible that the northernmost, rather isolated Swedish occurrences of *Stomis pumicatus* originated in this way, all the more so since it is flightless and occurs there as a markedly "cultural species." The same might hold for the functionally brachypterous *Pterostichus vulgaris*, which is "favored by culture," with regard to the records near Lk Pelkosenniemi and Lj Triostrova. Otherwise the "most isolated locality" is indicated in Table 37 (p. 680).

At any rate it is striking that so few species in Fennoscandia have a disjunct area that might be attributed to the erratic effect of anthropochorous transport. Otherwise such a phenomenon might be expected particularly in the case of flightless species, for which generally few modes of dispersal are available. Actually the contrary is true. Markedly disjunct areas chiefly characterize winged species, and in most cases these result from active flight and especially wind transport. The role of human culture in assisting dispersal lies more in the new biotopes and new *connections* between biotopes earlier isolated, chiefly in the Nordic woodland region (p. 641), than in the increase of possibilities for passive transport.

Other Dynamic Factors

Certain characteristics of an animal species, not mentioned earlier, may be dynamically favorable or unfavorable.

The soil-bound, flightless carabids show diverse ambulatory activity and the speed of running is highly variable. Unfortunately I have not made any measurements. In general the largest species—calculated absolutely—run faster; certainly no carabid can cover a longer distance per (longer) unit of time than the species of *Carabus*. Smaller, more or less constantly flightless species, chiefly *Calathus*, run as fast but have less stamina. Nevertheless, the

dependence on definite biotopes (the more or less pronounced stenotopy),
609 the daily period of activity, and exertion, etc. might decisively influence the active capability of dispersal of soil-bound species to the extent that simple measurement of the optimal (or average) running speed probably would not support any definite conclusions.

We often speak of the especially strong "*dispersal urge*" of some species. The expression is misleading. No animal has the urge—not even instinctive—to disperse in the geographical sense. The activity of the individual animal is caused by the feeling of discomfort in the momentary milieu or momentary internal state (hunger, etc.), possibly also by attraction toward positive stimuli, which the insects perceive chiefly by the olfactory sense. However, it is striking that the individuals of certain species show greater migratory activity than those of related species, which is usually impossible to explain. Furthermore that on an average they move farther from their "birthplace" and so have greater possibilities of continuous and rapidly expanding their area. The best examples among the Fennoscandian carabids are provided by the "transgrading" species listed below (p. 621). Even flightless species may undertake more or less long migrations. A mass migratory movement was observed by Gaunitz (1933) in *Carabus violaceus* (Lyl Sorsele). There were hundreds of individuals which migrated in the same direction toward a river bank, where they entered the water and were mostly drowned. Copulation was repeatedly observed, and it is possible that in this case a strong sexual urge had provided the stimulus for migration. In central Europe similar migrations of *Carabus auratus* have been observed (among others, by Horion, 1941, pp. 46–47). In one case (Barner, 1937, p. 24) it was emphasized that copulation between the migrating individuals did not take place.

The impetus for the locomotion of an individual—for a more or less pronounced "migration"—both in flightless carabids and carabids capable of flight may be mainly due to alterations in the environment. In particular, drying up of a biotope in summer might force markedly hygrophilous inhabitants to emigrate (p. 395). Excessive population density in carabids may rarely, if at all, lead to the same phenomenon (pp. 559, 654). However, it is clear that a high abundance at the biotope can produce a greater multitude of migrating
610 individuals and increase the prospect of a later meeting of the sexes in the new localities.

Barriers against Dispersal

It is evident that for every species of animals any uninhabitable biotope is a dispersal barrier. This question was touched on in the section on "Stenotopy and Eurytopy" (p. 563) and in connection with "dispersal as a result of cultivation" (p. 641). In northern Fennoscandia the *forests* have been the principal barriers—especially in earlier times. They are difficult to cross for all the

species incapable of living in them. But in this section we will consider only the two dispersal barriers that have played the biggest role in the colonization of Fennoscandia and in the advance of species within the limits of this region, the *sea* and the *mountains*. The dry desert, which can be decisive for their dispersal in other parts of the earth, is missing from our region.

The Sea

The ability of carabids to cover long distances by air and by water has already been considered (on pp. 573 and 598 respectively). The effect of these agencies is best studied by analyzing the insular faunas, of which a series of examples were offered (pp. 198 ff.). Here the area-limiting effect of the sea shall be illustrated by three especially clear cases.

We will inquire how far the following seas form area limits for a greater or smaller number of species of carabid (br = brachypterous, d = dimorphic species):

1. The Gulf of Finland

a. Species that occur in northern Estonia but have not reached the south coast of Finland.

Badister sodalis br	*Carabus coriaceus* br
Bembidion argenteolum	*Pterostichus anthracinus* d
B. litorale	*Stomis pumicatus* br.

b. Species that occur on the south coast of Finland but are not known in northern Estonia.

611

Agonum micans	*B. ruficolle*
A. munsteri	*Harpalus luteicornis*
Amara interstitialis	*Patrobus assimilis* br
A. littorea	*Pterostichus gracilis*
A. montivaga	*Tachys bisulcatus.*
*Bembidion grapei**	

The discovery of one or other of these species on the north coast of Estonia in a future more thorough exploration of that country might restrict this latter group. At any rate a basic difference is evident from the first group—which is missing from southern Finland. This group comprises 3 brachypterous and 1 dimorphic (chiefly brachypterous) species, and in addition 2 species of *Bembidion*, which have good flight capacity and therefore are little affected by anemochorous transport (p. 590). On the other hand, the group of species that have not been found on the southern shore of Gulf of Finland includes, with one exception, only species capable of flight, which

**Bembidion grapei* is constantly macropterous in the southern part of its area (Fig. 50, p. 402).

can easily be transported with the wind—also anemohydrochorously. The unexpected fact, that more species have remained on the northern shore than on the southern shore of the Gulf of Finland, which will probably be confirmed by a thorough exploration of Estonia, may be due to favorable wind conditions (p. 589) for anemohydrochorous transport toward southern Finland. It is uncertain whether in addition the "positive heliotaxis" of the insects (p. 592) has played a role.

2. The Sea Separating Sweden and Denmark (Skagerrak, Kattegat, Öresund)

The barrier formed here by the sea is frequently only partial, which is evident in many cases between Skåne and Sjaelland, in others between the Swedish west coast and Jutland. Such species are indicated with an "S" (= obstructed only in the south) and an "N" (= obstructed only in the north).

a. Species that occur in Denmark but have not (or have only partially) reached the opposite parts of Sweden:

612 *Anisodactylus nemorivagus*
N *Bradycellus verbasci*
N *Calathus mollis**
N *Calathus piceus*
N *Demetrias monostigma* br
N *Dromius melanocephalus*
Harpalus punctatulus
Patrobus septentrionis australis.

b. Species that occur in southern and/or western Sweden but which have not (or have only partially) reached the opposite parts of Denmark:

Agonum dolens
Amara littorea
Bembidion dentellum
N *B. quadrimaculatum*
B. semipunctatum
B. velox
S *Carabus problematicus* br
S *Cymindis angularis* br
Dromius angustus
S *Dromius fenestratus*
N *D. marginellus*
N *D. quadrinotatus*
Harpalus distinguendus
H. luteicornis
N *Lebia crux-minor*
L. cyanocephala
N *Licinus depressus* br.

It is striking that dispersal of only four species could be impeded by *lack of flight capacity.*

3. The Channel between the British Isles and Continental Europe

I am unable to give a complete list. The following list of species that are missing from the British fauna (at least as constant members) but have reached the opposite side of the Channel has been compiled from Sainte-Claire Deville (1930a, b) and Borchert (1938):

*In Jutland the otherwise dimorphic *Calathus mollis* is constantly macropterous (Fig. 28, p. 368).

Abax ovalis Dft. br	*Diachromus germanus* L.
A. parallelus Dft. br	*Dyschirius chalceus*
Agonum lugens	*Harpalus calceatus*
A. viridicupreum Gze	*H. distinguendus*
Amara montivaga	*H. modestus* Dej.
Bembidion elongatum Dej	*Leistus piceus* Fröl. br
Brachynus explodens Dft.	*Licinus cassideus* Fbr. br
Calosoma auropunctatum	*L. hoffmannseggi* Panz. br
Carabus auronitens Fbr. br	*Molops piceus* Panz. br
C. cancellatus br	*Pterostichus interstinctus* Sturm
C. coriaceus br	*P. punctulatus*
Cychrus attenuatus Fbr. br	*Trichotichnus laevicollis* Dft. d*.

613 The number of brachypterous species is strikingly high, but in central Europe they generally constitute a larger component of the fauna than in Fennoscandia.

A comparison of three sea straits reveals the following:

1. Gulf of Finland. In the outermost part > 45 km broad. Dispersal limit of 17 species (maximum), 12 of which are winged.

2. The sea between Sweden and Denmark. Width: Öresund > 4 km; Jutland-Sweden > 63 km. Complete or partial dispersal of 25 species, 21 of which are winged.

3. The Channel. Width > 31 km. Dispersal limit of 24 species (minimum), 13 of which are winged.

Evidently these species numbers are not directly comparable, since the length of coast, the richness of fauna, the question whether in some cases there may be existence limits rather than dispersal limits, etc. should also be considered. But we may be justified in stating that *the Gulf of Finland has been a more easily surmountable barrier for carabids than the straits between Sweden and Denmark and between England and the Continent*. And nevertheless, in both these cases firm land connections have existed during the postglacial period! The reason, as far as can be judged, is the much *lower salt content* of the water in the Gulf of Finland, such that anemohydrochorous—as well as purely hydrochorous—transport was possible to a far greater extent. This favorable circumstance applies to the Baltic Sea as a whole and may be the chief reason for its unexpectedly slight importance as a dispersal barrier.

The Mountains

Mountains need not be very high to pose a barrier to dispersal. Watersheds, even if they are geomorphologically poorly marked, represent boundaries which are difficult to cross *for aquatic animals and riparian species without flight capacity*. This is vividly illustrated in the case of fish by Ekman (1922,

*Dimorphic, according to Horion *in litt.*

pp. 463 ff.) and by A.M. Hansen (1929, p. 98). An example from the Fennoscandian carabid fauna is provided by the constantly brachypterous northeastern stock of *Bembidion transparens*, which has evidently not succeeded in crossing
614 the divide between the Arctic Ocean (including the White Sea) and the Gulf of Bothnia (p. 392, Fig. 45).

For other insects less closely associated with water, as well as for species that can actively or passively disperse through the air, the *Regio alpina* of the fjelds represents the most difficult barrier. It forms a nearly unbroken wall along the Scandinavian fjeld-range, which in the stretch extending from the extreme northern tip of Sweden into the province of Härjedalen coincides fairly exactly with the boundary of the kingdom with Norway. Farther south the main watershed bends toward the west and is responsible for the faunistic isolation of the Norwegian "western country."

The barrier formed *by the Scandinavian fjeld-range* is especially evident from the advantageous effect of the *passes*, shown in the map in Fig. 61 (p. 437). Let us first consider *the passes lying in the Regio coniferina*. Such passes are found only in two regions: 5 passes in Jtl and 3 passes in south-central Norway, connecting the Trondheim region and Romsdal with southeastern Norway. Clear examples are (br = brachypterous, d = dimorphic species):

1. Species that have crossed the watershed northward through the central Norwegian passes:

Amara tibialis	*Trechus discus*
Badister bipustulatus	*T. micros.*

To what extent migration through these passes has been in the opposite direction (southward) is discussed elsewhere (p. 770).

2. Species that have crossed the watershed through the passes in the central Jämtland (Storlien region),

a. Westward:

Agonum dolens	*B. obliquum*
A. micans	*B. quadrimaculatum*
A. piceum	*Pterostichus minor* d
Bembidion doris	

b. Eastward:

Bembidion nitidulum	*Leistus ferrugineus* br
B. virens	*Patrobus atrorufus* br.

615 The only passes farther north are in the *Regio betulina*. These were also utilized by some species incapable of living in the *Regio alphina*, at least not permanently. Examples are:

3. Species that have used the passes in southern Lapland (Åsl, Lyl);

a. Westward:

Agonum quadripunctatum	*Agonum sexpunctatum*

Amara ovata ? *Dyschirius thoracicus.*
Bembidion lampros d

b. Eastward:

Bembidion nitidulum *Patrobus atrorufus* br
B. virens *Trechus obtusus* br*
Leistus ferrugineus br

4. Species that have utilized the passes in northern Lapland (Tol)
a. Westward:

Tachyta nana

b. Eastward:

Bembidion virens *Leistus ferrugineus* br.

Of course, these examples are only the clearest cases. Without doubt many, more widely distributed species which avoid the *Regio alpina* have crossed the Scandinavian fjeld-range in one or both directions through these passes.

The above "pass ambulators" together comprise 22 species, 17 of which are constantly macropterous, 3 constantly brachypterous, and 2 dimorphic. Of the two last, *Pterostichus minor* has crossed the fjeld-range only as macropterous form (Fig. 43, p. 388), whereas *Bembidion lampros* has done so in both forms (Fig. 40, p. 384). So we have (as minimum value) 18 functionally macropterous and only 4 functionally brachypterous species that have used the passes.

An important conclusion can be drawn from this: For dispersal, even the carabids capable of flight, are dependent on the existence of continuous suitable biotopes. Although they are often driven out into such biotopes situated in new regions—chiefly by the wind—this apparently rarely results in permanent new colonies. This is indirect proof of the idea propounded above (p. 589) that long-distance transport of carabids in the higher layers of the air has very little dispersal significance.

The discussion on the faunistic effect of the Scandinavian fjeld passes considers only present-day conditions. It is well known, however, that during postglacial time, in the so-called "xerothermic period," the more favorable climate appreciably raised the timber lines in the fjelds (p. 687) and in this way allowed greater exchange of faunas between the two sides of the Scandinavian fjeld-range. A clear example of a faunal element that apparently utilized the then wooded passes is provided by the partly flightless species of eastern origin considered above (p. 405), which have an isolated relict-like area at the inner part of the Sognefjord in western Norway.

The advancement of forests into the fjelds affected the true alpine fauna adversely (p. 755).

**Trechus obtusus* was found in Hjd just above the timber line, but is certainly not a true inhabitant of the *Regio alpina*.

Final Remarks on Area Limits

Of prime importance for the correct representation of the area of an animal or plant species is the question whether or not its limits are throughout determined by existence factors. Is there a generalized solution to this? *Is it possible to conclude from the mode of occurrence of an animal or plant species at the border of its area whether an existence limit or a dynamic limit is involved*?

This question is of decisive importance for the discussions in subsequent sections. For if we believe at all we can reconstruct the course of history from the present picture of an area there are two essential preconditions: first, that not all area limits are produced by existence factors alone; second, that it is possible to decide whether in a given case an existence limit or a dynamic limit is involved.

The characteristics of a dynamic limit are:

1. The species is demonstrably in the process of dispersal, and the ascertainable alterations in area are larger than what can be explained by simulta-
617 neous environmental changes (primarily climatic). The species that are most clearly in process of expanding their area are considered below (p. 621).

However, in general it cannot be expected that a species in process of expanding an area should make such great progress that this can be established on the basis of collected material spanning barely a century. Other criteria must be applied.

2. In the case of an *existence limit*, especially if it is climatically determined, it is to be expected that the biotopes suitable for the species concerned will be scattered. This causes *reduced frequency*. On the other hand the abundance (the density of individuals) need not necessarily decline.

In the case of a dynamic limit, concentration in a few, widely separated surfaces is not to be expected. On the other hand an accelerating spread of individuals toward the periphery must ensue. Hence the consequence is *decreased abundance*—with the same or slightly reduced frequency.

3. If neither of characteristics 1 and 2 is ascertainable, the dynamic character of an area limit has to be tested simply by the exclusion method. If the limit is not found to correspond with any climatic line, if no edaphic, food habit factors, etc. can be cited, we can presume at least a dynamic limit. Examples are *Amara torrida* and other "north-eastern" species which are restricted to northern Scandinavia, although they there occupy an area extending from coast to coast with a more or less sharp southern limit; and *Bembidion nitidulum* and other "western" species, which have crossed over to the Swedish side through the fjeld passes and demonstrated that they are not dependent on the oceanic climate of western Scandinavia.

The difference between existence and dynamic limits is especially clear among the *dimorphic* species. If the macropterous form has advanced farther than the brachypterous form, it can be contended that the area limit of the

latter is a dynamic (provisional) limit (examples: Figs. 28, 35, pp. 368, 376). If both forms have reached the periphery of the area we are justified in speaking of a (more or less stable) *existence limit* (examples: Figs. 40, 41, pp. 383 ff.).

618 To the extent that the dynamic limit can be correctly singled out and judged, we get the most important key to antiquity—to the history of the area.

The clearest *existence limits* in Fennoscandia are the (mostly climatically determined) northern limits of the southern species. To give a general idea of their borderline, I compiled the map in Fig. 82. The species shown are markedly southern, with more or less continuous areas and, as far as can be judged, existence-ecological (climatically) determined northern limits. According to their northern limit on the east coast of Sweden they are divided into the following 6 groups:

a) Northern limit in Nbt (south of the Arctic Circle). 14 species (*Agonum versutum*, *Amara bifrons*, *A. ingenua*, *A. ovata*, *A. plebeja*, *A. tibialis*, *Calathus erratus*, *Cicindela campestris*, *Dromius sigma*, *Dyschirius politus*, *Elaphrus uliginosus*, *Lebia crux-minor*, *Pterostichus minor*, *Trichocellus placidus*).

b) Northern limit in Vbt. 9 species (*Agonum assimile*, *Amara consularis*, *A. famelica*, *A. similata*, *Carabus hortensis*, *Dromius marginellus*, *Harpalus pubescens*, *Pterostichus vulgaris*, *Trechus secalis*).

c) Northern limit in Ång. 6 species (*Bembidion gilvipes*, *B. unicolor*, *Carabus granulatus*, *Chlaenius nigricornis*, *Dromius fenestratus*, *Trechus quadristriatus*).

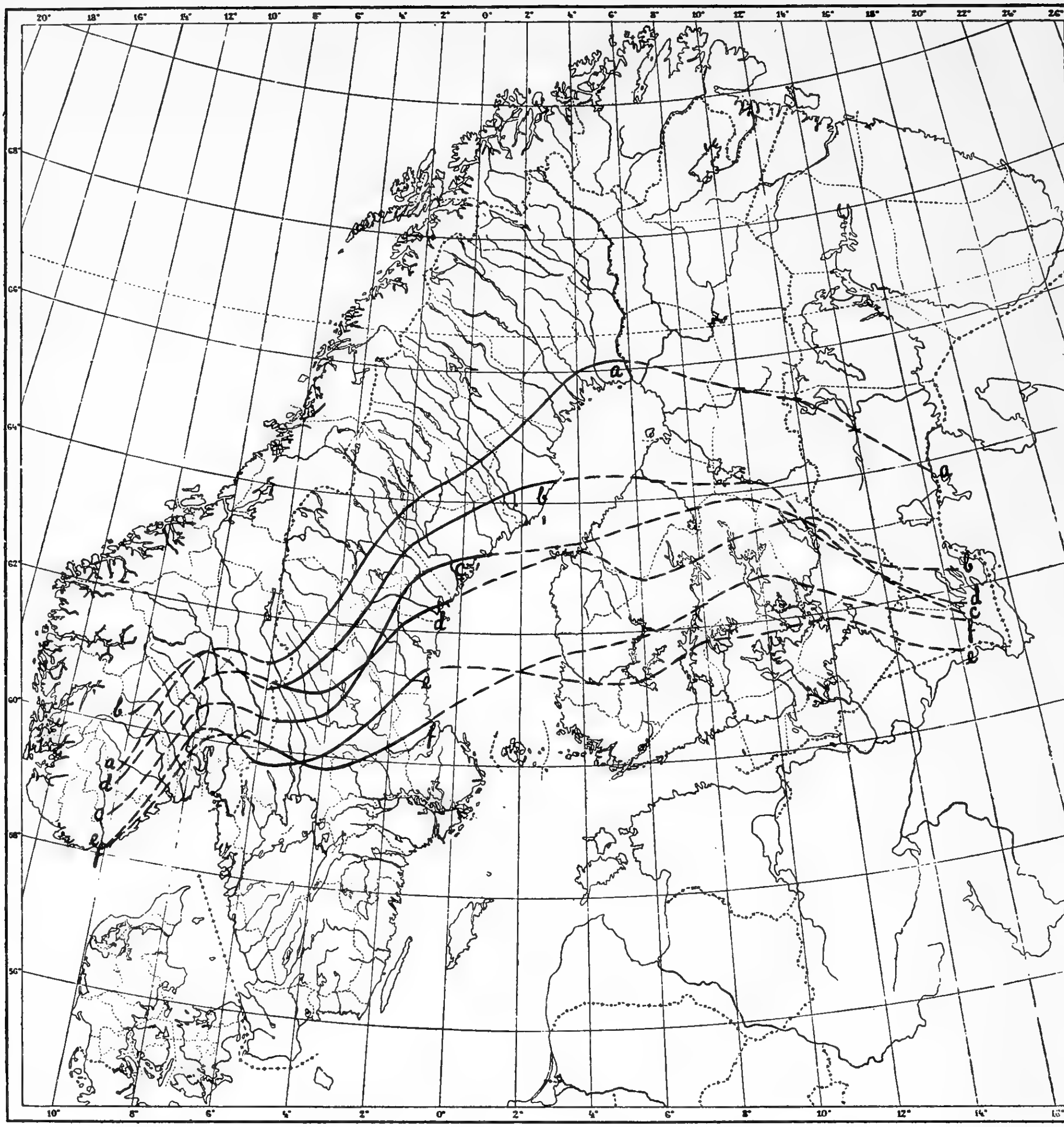
d) Northern limit in Mdp. 4 species (*Bembidion dentellum*, *B. ustulatum*, *Carabus nemoralis*, *Harpalus tardus*).

e) Northern limit in Hls. 16 species (*Acupalpus dorsalis*, *A. flavicollis*, *Agonum livens*, *A. moestum*, *A. obscurum*, *Amara aenea*, *A. curta*, *A. equestris*, *Anisodactylus binotatus*, *Badister bipustulatus* s.l., *Carabus arvensis*, *Dromius nigriventris*, *D. quadrinotatus*, *Harpalus distinguendus*, *Lebia chlorocephala*, *Notiophilus pusillus*).

f) Northern limit in Gst. 9 species (*Asaphidion flavipes*, *Badister peltatus*, *Bembidion articulatum*, *Bradycellus similis*, *Broscus cephalotes*, *Calathus fuscipes*, *Harpalus seladon*, *Oodes helopioides*, *Pterostichus cupreus*).

The mean northern limit of all the species in each group was calculated for every second meridian by interpolation. Isolated, probably more or less accidental records (for example of *Acupalpus dorsalis*, *Anisodactylus*, *Asaphidion*, *Chlaenius*, *Harpalus seladon*, *Oodes*, *Pterostichus vulgaris*) were ignored.

The "mean" limits drawn are intended to illustrate only the general char-
620 acter of an existence limit and do not justify any other conclusions. However, on an average the northerly position of the limits in Finland is striking (cf. pp. 459 ff.). Only in Sweden is the occurrence (distribution) of the species in each group somewhat uniform. In the two neighboring countries some ap-



619 Fig. 82. "Mean" northern limit of 6 groups of species having southern distribution:

a—14 species with Swedish northern limit in Nbt (south of the Arctic Circle); b—9 species with Swedish northern limit in Vbt; c—6 species with Swedish northern limit in Ång; d—4 species with Swedish northern limit in Mdp; e—16 species with Swedish northern limit in Hls; f—9 species with Swedish northern limit in Gst.

pear to be more "Atlantic," others more "continental" as they extend farthest north in Norway or in Finland. Hence the limits drawn in the map (Fig. 82) primarily reflect the distribution in Sweden.

Faunal History

621 **Faunal Changes in Recent Times**

There is no doubt that the Fennoscandian fauna is still in the process of change. In reading Gyllenhal's "Insecta Svecica" (1810–1827) one is struck not only by species that were evidently more abundant and more widely distributed in those days but more especially by the absence of a whole series of species that would certainly not have escaped the attention of this sharp-eyed researcher if they had been as frequent and abundant then as now. In the geologically brief period of one century, several species have in fact immigrated to Fennoscandia and many have considerably expanded their area. It is of course not very easy to provide evidence for this, since in our region really intensive coleopterological work has been carried out only in recent decades. But in some cases at least the approximate course of the area displacement seems clear, and the total picture gives the distinct impression that, in spite of (partly because of) the increasingly rapid destruction of the natural landscape, the Fennoscandian fauna has undergone more additions than losses, i.e. the fauna has become richer in species. This is the characteristic of a Quarternary glaciated region. This "mobile" element of the Fennoscandian fauna is best divided into the following categories:

I. INCREASING SPECIES

1. *Transgrading species*. These are more or less accidental migrants that do not reproduce within the region, at least not regularly. They are the counterparts of *Acherontia atropos*, *Pyrameis cardui* and *P. atalanta*, *Phytometra gamma* and other Lepidoptera, although the distances covered by flight are mostly much shorter. Strictly speaking there is no actual area enlargement (on the contrary,
622 in *Calosoma sycophanta* a postglacial area diminution has taken place, see p. 674), but the occasional advances often give an impression that makes them difficult to distinguish from the actual immigrants.

The doubtful species are:

Agonum gracilipes	*Bembidion octomaculatum*
Amara crenata	*B. striatum*

? *Calosoma auropunctatum*
C. denticolle
C. investigator
C. sycophanta
(*Carabus auratus*)
? (*C. monilis*)
Chlaenius costulatus
C. sulcicollis
? *Dromius quadraticollis*
Dyschirius neresheimeri
(*Pterostichus madidus*).

The species that have arrived anthropochorously are given in parentheses. Partially transgrading species are:

Harpalus calceatus *H. griseus.*

Both appear to have permanently colonized only southern Skåne (see also Landin, 1948), but occasionally undertake long migratory flight. Definite "swarming years" have not been proved.

Other species which within the subareas of the region, chiefly on the islands, occur as accidental migrants, are ignored here. An idea of the extent of this phenomenon has been provided by Palmén (1944).

2. *Late immigrants*. As far as can be judged, these species have immigrated into Fennoscandia during the last hundred years, and have become resident members of its fauna:

Amara fusca
A. majuscula (Figs. 83, 84)
Bembidion lunulatum
Bradycellus verbasci
Clivina collaris
Harpalus puncticeps (Fig. 85)
? *H. rupicola*
Lionychus quadrillum
Stenolophus mixtus.

Among these immigrants, *Amara majuscula* represents an especially clear case. The first records within the region (and the whole of Europe) were published in the year 1942 (Stockmann, 1942; Har. Lindberg, 1942). Actually, the species had already been collected in Finland in 1928, in Sweden even in 1917 (Skå Åhus). Harald Lindberg (1942, 1943) regarded *Amara majuscula*, as also *A. crenata* and the curculionid *Gronops inaequalis* Boh., found at the same time in Al Kökar, as old relicts within the Baltic region (as "pseudorelicts"
623 on Kökar). This assumption is certainly erroneous. These are late immigrants, and the record of a single specimen of *Amara crenata* is evidently the result of an accidental transgression. In the case of *Amara majuscula* it is possible to trace the immigration almost from year to year (Figs. 83, 84). It occurs as an invasion from the southeast on a broad front, and it is much to be regretted that on account of the political conditions no information on a simultaneous or even earlier occurrence of the species in the Baltic states was available. But Makólski informed me in personal correspondence that near Warsaw on August 3, 1927, *A. majuscula* abruptly undertook an enormous nocturnal approach flight. Earlier the species was unknown in Poland. In company with it was the likewise alien species *Harpalus zabroides* Dej., which was not found

again in this region. On the other hand, *Amara majuscula* stayed on for many years and undertook more mass flights, for instance, in 1947. Concerning a new record of *Gronops inaequalis* in drift material off the island of Fårön, see Palm, 1947 (p. 177).

None of the other immigrants shows the clear, regular immigration of *Amara majuscula*. It is of course clear in the case of *Harpalus puncticeps* (Fig. 85). In April 1888 several specimens of this species were collected near Hll Särö. It was never found again there even though this narrowly delimited locality was one of the favorite haunts of earlier Göteborg entomologists (Sandin, I.B. Ericson, and others). Apparently the above occurrence represents the result of a single immigration, which probably took place the preceding summer, and did not lead to permanent colonization. The species was found again in Sweden only in 1920, significantly in the extreme southern corner of Skåne. Since then, especially during the thirties, it has spread north and east, since 1944 even to Öland.

With respect to the other immigrants the following facts may be mentioned:

Amara fusca. The first definite Swedish record on the island of Ven in 1934; eight years earlier it had been discovered on Bornholm (West, 1930, p. 447), but the very first Danish record at all (ørholm) was made as late as 1919 (West, *in litt*.). Up to 1946, the species was known in Skåne from 10 localities. It was found at several of these repeatedly and in fairly large numbers. It seems out of the question that it should have escaped the attention of earlier entomologists in these well-explored regions. Later, an increase in the *Amara fusca* population was recorded even in northern Germany (Nürnberg in Horion, 1941, p. 261).

625 *Bembidion lunulatum*. The first Swedish record (Skåne) was made in 1911, and on Öland in 1921. It is conceivable that this comparatively inconspicuous species, leading a solitary and fairly concealed life, was earlier overlooked, but it is striking that during a period of less than 30 years (1911–1938) 6 localities were discovered in Skåne. A new immigration seems highly probable. In Denmark this species was discovered in 1909 near Copenhagen (West, *in litt*.).

Bradycellus verbasci. Only two records, in southern Skåne, in 1936 and 1939. In Denmark, too, the species seems to have greatly increased in the last 30 years. It was unknown to Schiødte (1841, 1870): the first record (Roden Skov) was made in 1886 (West, *in litt*.).

Stenolophus mixtus. This species was of course repeatedly found in the nineties near Skå Skabersjö, but since then it has considerably spread and has
627 reached northern Skåne. 1 specimen was found in 1947 in Öland. The first Danish record (Fyn) goes back to 1871 (West, *in litt*.). The late immigration is still more evident east of the Baltic Sea, since the species was discovered in Finland only in 1927 (Hellén, 1929, p. 95), and in Estonia in 1933 (Haberman,

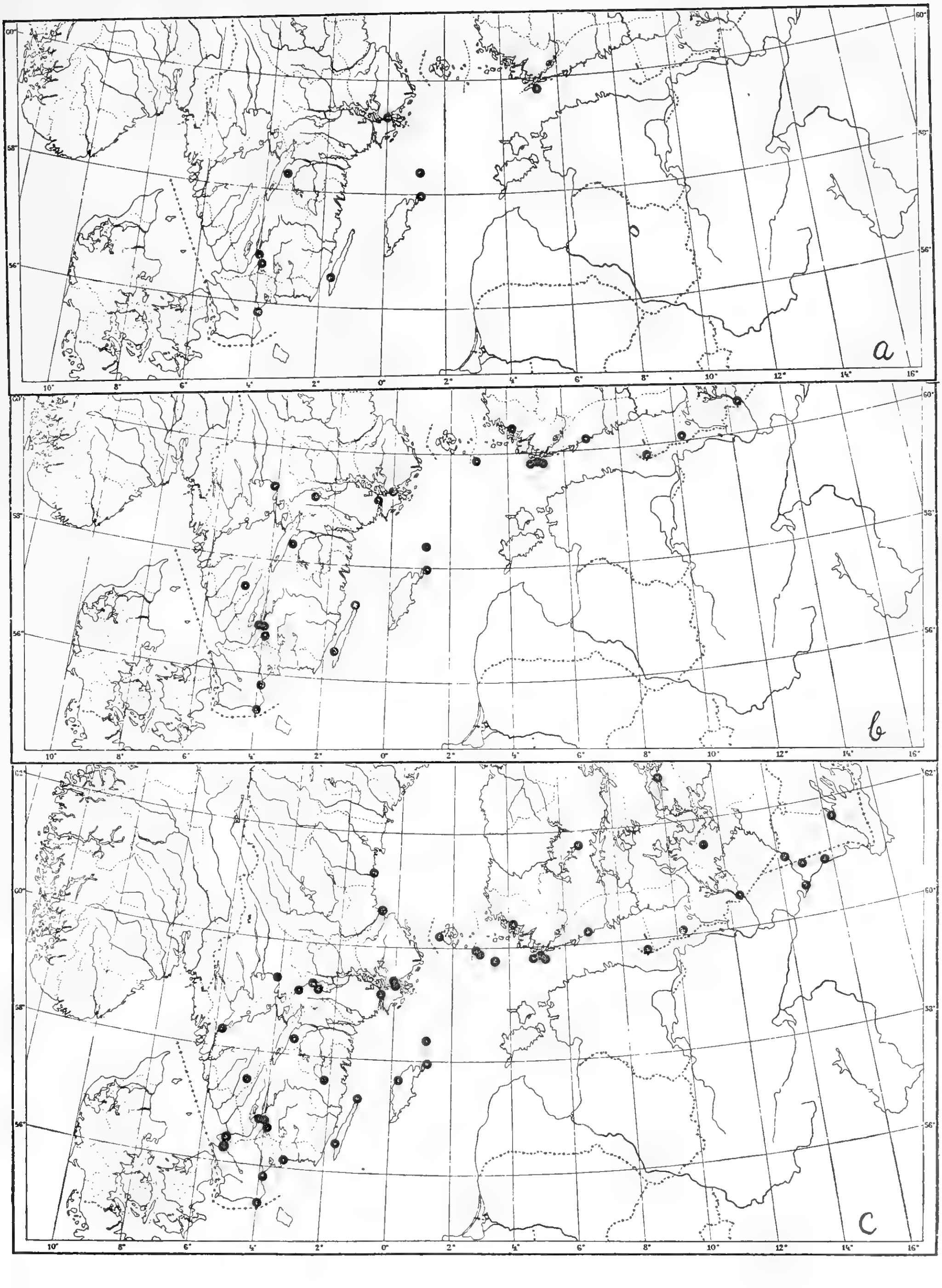
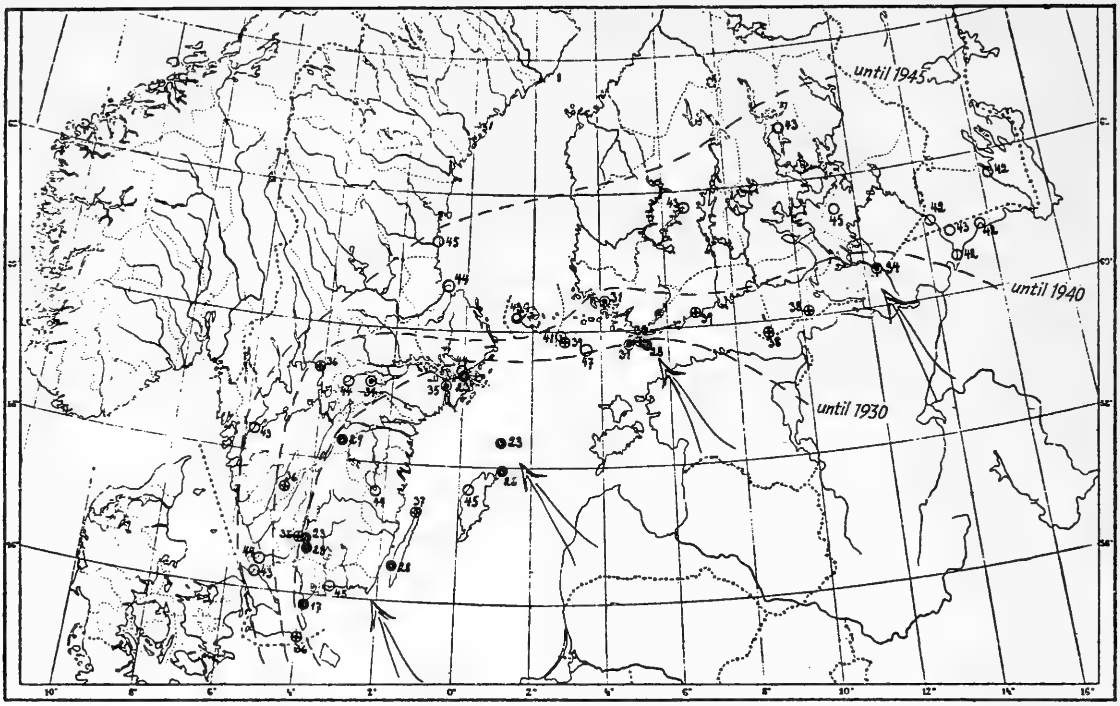


Fig. 83. *Amara majuscula*. a—Until 1930; b—Until 1940; c—Until 1947.



625 Fig. 84. *Amara majuscula*. The first collecting date for every locality is shown. Black circles—Until 1930; Spotted circles—Until 1935; Crossed circles—Until 1940; Blank circles—Until 1947.

1935, p. 176). In the Leningrad region, however the species was already known since olden days.

The two remaining species (without question mark) may be considered with fairly high probability of anthropochorous arrival. In the case of *Clivina collaris*, which was found to be exclusively synanthropous in our region, even in greenhouses in the environs of Göteborg and Stockholm, the situation seems to be clear.—*Lionychus quadrillum*, which was first discovered in 1945 in its only north European locality to date near Nke Örebro, where it occurs in astonishing numbers, in my opinion may have been similarly displaced (but see also p. 589). After discussing all the possibilities in this connection, Heinze (1947) leaves it open whether *Lionychus* should be considered as a relict or as a late immigrant. But the Örebro region, chiefly thanks to the ardent efforts of Anton Jansson, has been so thoroughly explored that the carabid could scarcely have been overlooked earlier. It is just the occurrence in large numbers in all three years 1945–47, which were *meteorologically very unusual*, that decisively contradicts the idea that *Lionychus* must have led a concealed life since olden

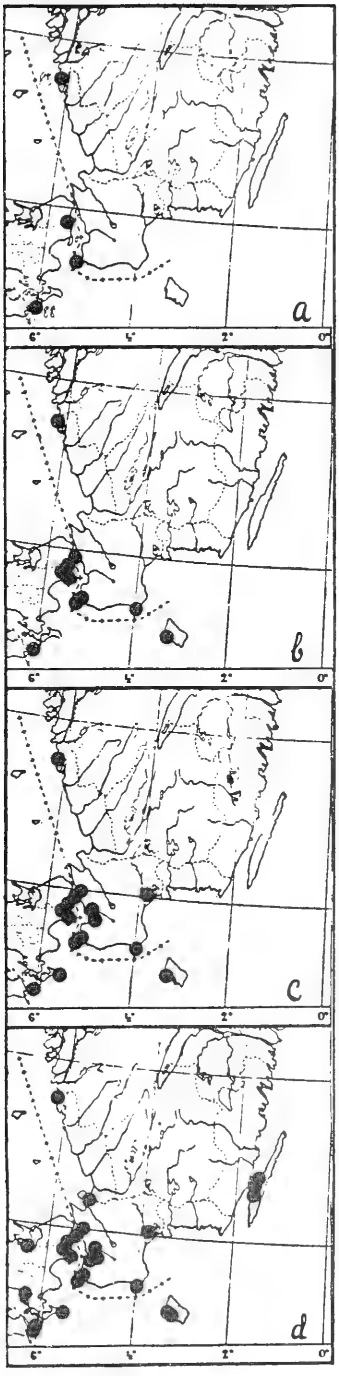


Fig. 85. *Harpalus puncticeps*.

a—Before 1933; b—Before 1937; c—Before 1939; d—Until 1947.

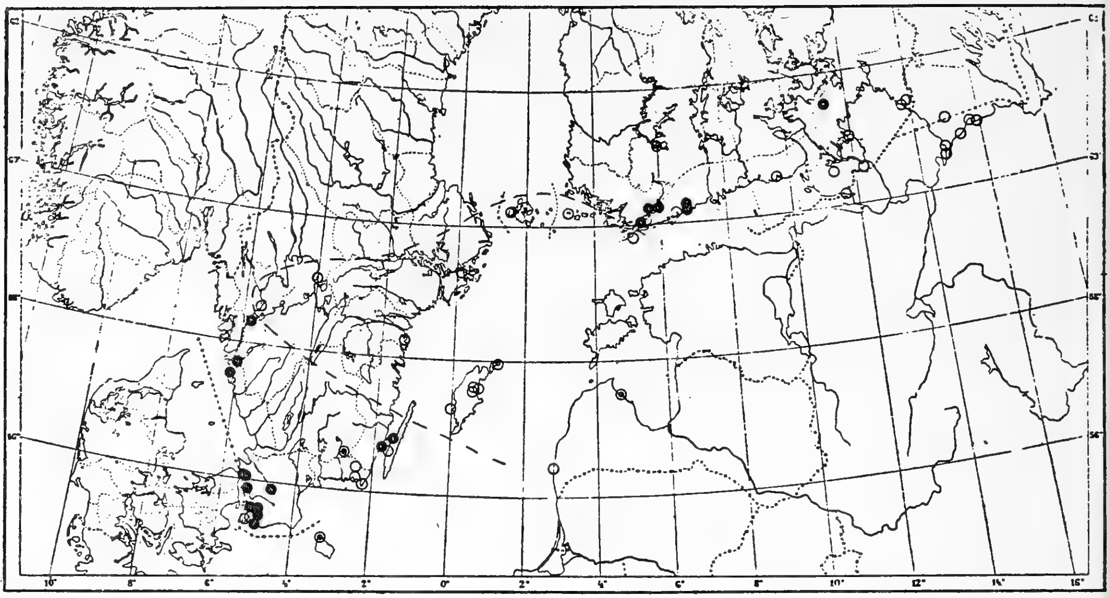


Fig. 86. *Acupalpus exiguus.*

628 The region colonized after 1930 is delimited by broken line. Black circles—Before 1920; Spotted circles—1920–1930; Blank circles—After 1930.

times as a relict to appear suddenly in such large numbers.

There remains *Harpalus rupicola*, which is mentioned here with reservations. This species, known within the region only on Öland and Gotland, is now one of the truly characteristic animals of the loam-mixed weathered limestone soil on the latter island, where it has wide distribution and is almost frequent at places. Strange, then, that this species was not found by any of the assiduous entomological collectors of the last century (especially Boheman): the first record was in 1905. On Öland it was only found in 1934 (until now only 4 specimens). The distribution of the individuals of *H. rupicola* collected in different five-year periods, as far as is known in Sweden, seems to be typical of a newly immigrated species as well, which is still in the process of continuous increase:

Before 1923	1923–27	1928–32	1933–37	1938–42	1943–47
1	13	20	36	50	99 specimens

In Denmark, *H. rupicola* is at least partially older, since it was found in Møen already in the middle of the last century (West, 1930, p. 447).

625

Fig. 87. *Agonum micans.*

Black circles—Before 1900; Spotted circles—1900–1914; Crossed circles—1915–1929; Blank circles—Later finds. The age of records in the Trondheim region is uncertain, but the species was first mentioned there by Lysholm (1937).

628 Finally, *Notiophilus rufipes* and *Pogonus luridipennis* are probably late immigrants. Concerning *Amara montivaga* see below.

3. *Other species in the process of area expansion*. As members of the Fennoscandian fauna these are of course older than the "historical" time for which their arrival could be proved, but within the limits of our region they have expanded their area within a conceivable period, especially north. Their limits are pronouncedly dynamic.

Shifting boundaries within the Fennoscandian region are so common that it is impossible to list all the species for which such displacement might be assumed with fair probability. One's verdict depends on the importance one attaches to the absence of a particular species in older collections from one
630 or other part of its present area. Mostly a pronounced tendency to dispersal is ascertainable only in species that have indubitably demonstrated it in recent decades.

The following list is to be taken as a selection of more or less typical cases:

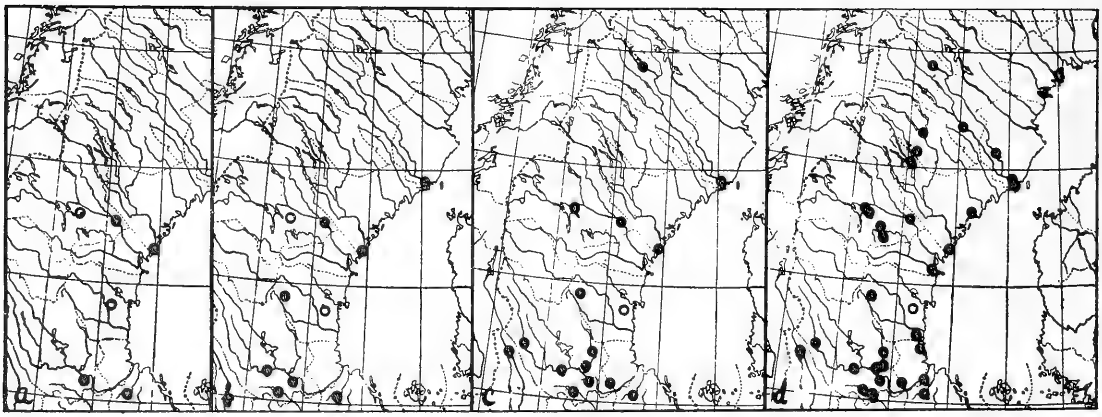
Acupalpus exiguus (Fig. 86). Especially in Sweden.

Agonum micans (Fig. 87). Throughout the region (see below).

**Amara ingenua* (Fig. 88; see also pp. 525, 538). At least in northern Sweden.

**A. montivaga* (Fig. 89). At any rate in Sweden (see below).

**A. municipalis*. At least in Sweden. In Norrland only one record from Hls during 19th century.



630 Fig. 88. *Amara ingenua.*

Swedish localities north of latitude 60° N. a—Until 1910; b—Until 1925; c—Until 1935; d—Until 1947. Blank circles indicate old provincial records.

A. similata. All localities in Sweden north of latitude 61° N, in Finland north of 63° N, were recorded in this century.

**Bembidion obtusum*. In southeastern Sweden.

B. transparens. In Sweden. See map, Fig. 45 (and p. 389).

**Carabus nemoralis*. Especially in Finland (see below).

Dichirotrichus rufithorax. In Sweden (see below).

Dromius linearis (see below).

D. melanocephalus. All boundary records on Skåne were discovered in the thirties. Increased frequency in Denmark, in the last 100 years was also evident (West, *in litt.*).

631 *Harpalus punctatulus* (Fig. 90). In Finland (see below).

Odacantha melanura (see below).

(*)*Trechus discus*. All Finnish and Swedish records north of 59° were made in this century.

(*)*T. quadristriatus*. All localities in Sweden north of 61°, in Finland north of 62°, were recorded in this century.

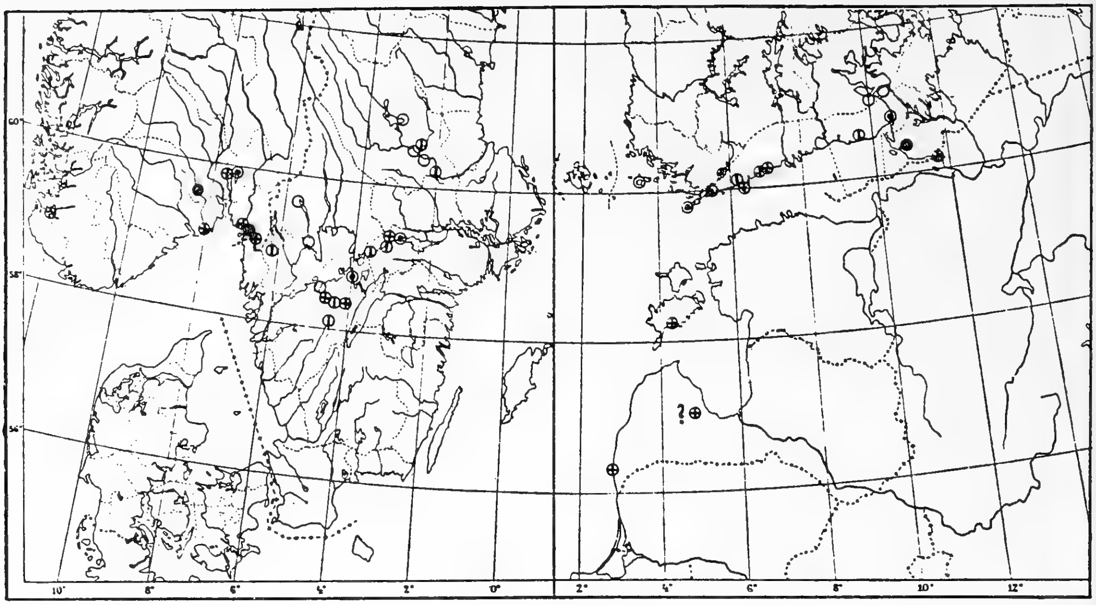
Species markedly favored by culture are marked with an asterisk (*).

Some of these 16 species deserve further consideration.

632 *Agonum micans*. There is no doubt that this species has sharply increased in Fennoscandia during recent decades and has expanded its area. However, no one-sided new immigration seems to have taken place. On the contrary, there may exist isolated older centers, such as in Denmark and Skåne (fossil record from the "warm period"†; p. 666), in the Mälar Lake region, in southeastern Norway and in southeastern Finland, whence the species has spread widely, especially in the thirties. But it is impossible at present to decide on the origin of the very isolated stock around the northern end of the Gulf of Bothnia.

Amara montivaga. The distribution of this species in Scandinavia seems to be unique. The area seems to be completely isolated, since the species is missing from southern Sweden and from Denmark and occurs very sporadically in northwestern Germany (Horion, 1941, p. 254). Eastward there is no connection with the Finnish area. The species undoubtedly immigrated late into Sweden; the oldest record (Nke Örebro) goes back to 1904, and the occurrence in Dlr is most recent (known since 1935). As surmised by Munster (1927, p. 288), it is possible that the species in Norway is also a late immigrant introduced with commerce; it was of course collected there (near Halden) before 1870, and it is not inconceivable that it was overlooked earlier by the few older Norwegian coleopterists. In Finland several records, not only on the southwest coast but also in the inland (north to 62°), date from the last century, and it is not possible to establish any pronounced dispersal in recent decades. Nevertheless the Finnish subarea is also completely isolated, since there are no records at all of this very conspicuous species from the Baltic

†(cf. p. 687; suppl. scient. edit.)



631 Fig. 89. *Amara montivaga.*

Black circles = Before 1890; Spotted circles = 1890–1909; Crossed circles = 1910–1930; Hatched circles = 1931–1936; Blank circles = 1937–1947.

Fig. 90. *Harpalus punctatulus.*

Black circles = 1919; Spotted circles = 1928–1934; Crossed circles = 1935–1939; Hatched circles = 1940–1944; Blank circles = 1945–1947.

states or from the adjoining parts of Russia (not even from eastern Karelia).

Carabus nemoralis. This is now by far the commonest species of *Carabus* in the southern parts of Fennoscandia. But it was not always. This species was not known to Linné, although his contemporary De Geer (1774, p. 89) described it under the name "*violaceus,*" probably from Swedish material. Distribution data are provided neither by him nor by Paykull (1790, p. 17; 1798, p. 102; "*hortensis*"), Gyllenhal (1810, p. 59) writes only "*minus frequens*". The following interesting information was first provided by Thomson (1857, p. 7; in summarized form 1859, p. 9): "According to a written communication from
633 Prof. Boheman, this species shows a peculiar distribution in that it is common on Skåne and near Stockholm, but is not found in the provinces lying in between" (translated from the Swedish). Since Boheman had collected assiduously in the parts of Sweden he had in mind (Ögl, Små, Ble, Hll, etc.) we may accept his judgment. On the other hand the expression "not rare" and "Sk.-Lpl." in the later contribution by Thomson (1885, p. 2) is not only difficult to

understand but also rather inconsequential, since it is a notoriously superficial synopsis. Grill (1896, p. 2) writes "Sk.-Gestr.", and even today the northern limit of the continuous area lies in southern Hls; farther north there is only the record of a single specimen near Sundsvall around the turn of the century. In Finland the increase of *C. nemoralis* later is still more pronounced. Of course it was already known from there more than 100 years ago (C.R. Sahlberg, 1834, p. 213), but it was known to J. Sahlberg (1873, p. 60) from only three Finnish localities (Vasa, reported by Wasastjerna, must be excluded; see Part I, p. 13). All of the five northernmost widely separated localities were discovered after 1932. In eastern Karelia it was only discovered in 1944 (Palmén, 1946, p. 19). On the other hand the species seems to have remained rather stationary in Norway. In the northernmost known localities (Smöla; Trondheim) it was already known in the 1870s. Of course its abundance in this region has perceptibly increased in recent decades (Born, 1926, p. 71; Lysholm, 1937, p. 144). Finally, attention may be drawn to the fact that *C. nemoralis* was not found in fossil form either in Denmark or in Fennoscandia, as it was in eight other species of the genus.

Dichirotrichus rufithorax. The occurrence of this species in Scandinavia exclusively in the central Swedish lake region is striking, as also its exclusively synanthropous occurrence in our region, since it lives only on cultivated land in or around fairly large human settlements. The oldest Swedish record is from Stockholm (before 1868), the most recent records from the westernmost regions (Nke Örebro, 1937; Vrm Kristinehamn, 1945; Varpnäs, 1947; Ögl Linköping, 1947). Late immigration to Sweden must be assumed from the direction having the only connection, i.e. from Finland. In this country the species does not occur quite so synanthropously and has had a wider distribution since earlier times, especially in the southwest (C.R. Sahlberg, 1834, p. 260).

634 *Dromius linearis*. It is uncertain whether this species actually expanded the limits of its Swedish area during the last century, since even in the northern localities such as Vgl Kinnekulle and the Stockholm region, it was discovered as early as the middle of the preceding century. In any case, the species has greatly increased in frequency and abundance. In older collections it is found in large numbers only from Öland, and in Skåne it was a great rarity for a long time (Thomson, 1859, p. 227). It is possible that the striking increase has resulted from an altered mode of life (or from immigration of an ecologically different stock). At present, *D. linearis*, namely, shows its maximum abundance in *Psamma* and *Elymus* hummocks of sandy shores, but this occurrence is mentioned in the literature (also in foreign literature) rather late (as far as I have been able to trace it, first by Jansson, 1913, p. 383; see also Larson, 1939, p. 431; Horion, 1941, p. 336; there is no indication in this connection in Burmeister, 1939, p. 193). Greater abundance also seems to be indicated in Denmark (cf. West, 1940, p. 48, with Schiødte, 1841, p. 96) and in north-

ern Germany (Horion, l.c.). In Finland *D. linearis* was found late (1921) and only in the southwestern Skargård. The doubtful occurrence in Estonia makes immigration from Sweden almost certain (p. 239).

Harpalus punctatulus. The occurrence of the species in Sweden and Finland is basically different. In our region it has remained restricted to Öland and Gotland constantly and uninterruptedly for more than 100 years. In Finland it is a very late immigrant, having apparently immigrated partly from Estonia and partly across the Isthmus of Karelia (Fig. 90). A certain increased abundance has been noticed on Öland and Gotland over the last two decades, but an area expansion in Sweden has not taken place so far.

Odacantha melanura. In this case, too, greater abundance is more evident than any actual area expansion. In some cases there undoubtedly has been new colonization of localities. Thus *Odacantha* was never found earlier along the Ringsjön in Skåne, one of the best explored regions of this province since olden times, but was discovered there in 1939 and later recorded again. In the environs of Hälsingborg it was only recorded in 1915. Also in Blekinge and Västergötland, as well as on Gotland and Åland, all the records date from the last 20 years. However, in addition to Skåne, there are older centers on Öland and in the Mälar Lake region. In Finland the species occurred
635 at least accidentally more than 100 years ago near Helsinki (C.R. Sahlberg, 1834, p. 268). *Odacantha* thus seems to represent a case analogous to *Agonum micans* (see above).

Finally, attention may be drawn to two pairs of species for which I have earlier, in another context, surmised a comparatively late area expansion.

Amara erratica and *A. torrida* (Holdhaus and Lindroth, 1939, p. 261; Lindroth, 1939, p. 246). They possess a nearly identical, markedly northeastern distribution, with a southern limit in Scandinavia running from coast to coast between latitudes 65° and 66° N. This represents not an existence limit but a dynamic (historical) limit. Both are probably to be considered as postglacial immigrants (but see p. 733). It is uncertain whether any evidential importance can be attached to the fact that the southernmost inland records of both species in Sweden were made late (after 1924), since just these parts of Lapland were insufficiently explored earlier.

Demetrias imperialis and *Oodes gracilis* (Lindroth, 1943a, pp. 139–140). In the Stockholm region both species were discovered early, *Demetrias* already before 1810, *Oodes* in 1863. In both cases it was a long time before they were rediscovered in Sweden, and indeed in the same region, *Demetrias* in 1903, *Oodes* in 1922. During subsequent decades, chiefly in the forties, they were more and more frequently collected, mostly together, and farther away from Stockholm. This noticeable change cannot be explained solely by the less intensive earlier collecting activity in the Stockholm region; a sharp increase in the two species is undoubtedly a fact. The unexpected occurrence of the species of *Demetrias* in 1946, both on the island of Fårön (Palm, 1947, p. 171;

also rediscovered in 1947), and along the south coast of Lolland in Denmark (West, 1947, p. 17) is of course the result of immigration from other directions. But it proves that the external conditions, such as the climate, have become favorable for this insect in recent years. For these two species, see also p. 691.

II. DECREASING SPECIES

In the past century, on account of natural causes, just those species have become scarcer (or even extinct) that are dependent for their existence on
636 undisturbed "virgin forests" (for example, Saalas, 1939). Typical cases of this kind are not met with among the carabids. It is generally not easy to think of particular species that have unambiguously decreased in numbers or have even become extinct in Fennoscandia in "historical" time (entomologically speaking). The following species may be mentioned with fairly high probability:

a. Species avoiding "culture" (with northern distribution):

Agonum bogemanni *Harpalus nigritarsis.*
Amara nigricornis

b. Species indifferent to culture (with southern distribution):

Dolichus halensis *Pterostichus punctulatus.*

c. Species favored by culture (with wider distribution):

Agonum quadripunctatum *Pristonychus terricola*
Bembidion quinquestriatum *Sphodrus leucophthalmus.*

An example of Lepidoptera which, possibly for climatic reasons, has apparently become extinct in Sweden is *Pararge achine* Scop. (Kjellander, 1943).

Causes of Recent Area Alterations

To explain area displacements in recent times the following five reasons may be adduced (cf. also Benick, 1947).

1. *These alterations are simply exponents of the normal postglacial immigration of animals into a Quaternary glaciated region.* There is no doubt that such immigration has been continuously taking place in Fennoscandia, i.e. that in particular the northern limits of a considerable number of species are determined by *Dynamics*. The Fennoscandian fauna is actually characterized by a pronounced *lability* (Ekman, 1922, pp. 579–580). Even with regard to the fauna of Holstein, Warnecke (1929, pp. 51 ff.) thinks, the late, rapid immigration of several lepidopteran species is only a consequence of "normal" postglacial area expansion. But are these "normal" displacements actually perceptible from observations spanning only decades, at the most one and one-half centuries?

It can be argued that for an insect that has immigrated from the south and is climatically less susceptible, on an average nearly 15,000 years were at its disposal to reach its actual northern limit in Fennoscandia (Table 36,
637 p. 661) from a glacial refuge in Central Europe. Assuming that this limit is located somewhere in central Scandinavia (near latitude about 63° N), and that the species in question therefore tolerates a high-boreal climate, it can be surmised that it survived the last glaciation not far from the southern edge of Würm ice somewhere in present-day southwestern Germany. The distance from the assumed present northern limit, including the detour around the Danish islands which were once firmly joined with the mainland, might be about 1500 km. A rough calculation gives an average linear area expansion of 100 m per year. The last phase, the stretch from the Stockholm region up to the present northern limit, about 400 km, could have taken about 9500 years. That would mean an average of only 42 m per year.

These calculations, pretty far from reality—they ignore the periodic changes in dispersal trends caused by other factors—evidently hold only for ideal cases. Flightless insects in particular come across diverse *barriers* (the Danish straits after the Ancylus period, the Närke strait during the Yoldia period, etc.) and the immigration assumes a more erratic character. Some of the Ice Age refuges were probably farther away. Nevertheless, we may be justified in arguing that the normal speed of postglacial migration is not of a magnitude to be perceptible by direct observation in a matter of decades.

Rapid migrations such as those described above (and partly mapped) must be due to special causes which influence, positively or negatively, either the capability of dispersal or the existence possibilities of an animal.

2. *The area alterations are caused by man*, either by assisting in dispersal of the animal directly or indirectly, or by cultivation of the land which provided new living conditions.

a. That a species was transported by man is beyond doubt only in those cases where a clearly accidental occurrence in an alien region is involved. The following species of our fauna belong to this category:

Carabus auratus   *Pterostichus madidus.*

Probably falling in this category we also have the following species, which have been resident for a somewhat longer period:

Carabus monilis   *Lionychus quadrillum.*

638 Given their strictly synanthropous habits, at any rate in our region, the following species must also have arrived anthropochorously:

Clivina collaris   *Sphodrus leucophthalmus.*
Pristonychus terricola

It is highly probable that *Carabus nemoralis* and *Dichirotrichus rufithorax* (see p. 632) also originally arrived with man, although in the case of the

Carabus species this event occurred far back in time. It was also transported from Europe to North America.

Such sudden, erratic faunal alterations take place in no other way than by transportation of species with human traffic. This is due not only to the rapid, convenient possibilities of transport with modern means of travel, even over very long distances, but also to the well-known fact that animals transported to quite new regions have shaken off their natural enemies and may then reproduce undisturbed. Applied entomological literature provides many current examples.

The Fennoscandian carabid fauna includes no anthropochorous immigrants that have multiplied explosively; however, among other Coleoptera mention may be made of: *Philonthus rectangulus* Sharp (Har. Lindberg, 1937; Benick, 1947; native to East Asia); *Lathridius nodifer* Westw. (Holdhaus, 1927–28, p. 613; probably native to Australia); *Ptinus tectus* Boield. (König, 1936; native to Australia); *Tribolium destructor* Uytt. (Kemner, 1936; according to Hinton, 1948, p. 16, probably native to East Africa); certainly *Bohemiellina paradoxa* Machulka (Jansson, 1947), whose country of origin is unknown.

We have already discussed the significance of anthropochorous dispersal for carabids in general (p. 606).

b. With the exception of the fjeld regions and the far north, the human influence has had a decisive impact on the landscape of Fennoscandia. Especially in the south this took place quite early on and to a greater extent than generally assumed, as shown by Iversen (1941) with regard to Denmark.

Some carabids were negatively affected. Among the above-mentioned species (p. 636) that have decreased in recent times the 3 species under "a" were adversely affected, possibly directly by cultivation of the land and rational
639 utilization of the forest. For *Agonum bogemanni*, to a lesser extent for *A. quadripunctatum* (as surmised in Part I, p. 48) the decline of the old method of clearing forests by burning (Swedish: svedjeburk) may have exercised a great influence. This is supported by the fact that the last two records of *Agonum bogemanni* in Fennoscandia (1943 and 1944) were made during the war in eastern Karelia and in the Isthmus of Karelia, where the forests were extensively burned down by gunfire. *A. quadripunctatum* was abundant there in some places.

The 3 remaining species included above (p. 636) under "c" are of course strongly synanthropous (in our region even anthropobiont, bound to houses) but they live in old unhealthy buildings whereby their living conditions have become very difficult.

It is a puzzle why *Dolichus* and *Ptrostichus punctulatus* ("b", p. 636) have become scarcer. In Germany they seem to be unaffected by cultivation of the land.

Attention should also be drawn to an ecological group whose existence has been more and more seriously threatened in recent decades, namely, the *steno-*

topic riparian species. One after another our larger rivers are being regulated for the construction of electrical power stations. The natural water level with its more or less regular fluctuations is terminated, often considerable stretches of the water course are dammed up for water storage and the original banks submerged. All this means a series of catastrophic changes for the fauna associated with the waterside. Th. Palm told me that the fauna has changed out of recognition along the river Indals near Jtl Bispgården since our visit to that place in 1930 (Lindroth and Palm, 1934, p. 29). Probably in the near future some of the stenotopic riparian species (in the genera *Bembidion*, *Dyschirius*, etc.) will be exterminated along all river systems.

As to whether or not some species of insect from larger or smaller regions can be exterminated as a result of the collecting activity of entomologists, those responsible for this activity differ. At the worst this might happen in the case of diurnal especially conspicuous Lepidoptera, particularly if they have a short flying time and are also locally restricted from the very beginning. Given the
640 last stipulation, I doubt even the intensive, quite professional collection of butterflies from time to time for export to foreign insect dealers, especially in the Abisko region in Lapland, has perceptibly influenced the composition of the fauna. My opinion that at least with respect to the carabids the most intensive collection activity is inconsequential from the viewpoint of conservation of the species, was illustrated earlier (1948c, p. 45) with an example: Near Greby (Räpplinge parish) on Öland in June, 1946 all the detectable material of *Cymindis humeralis* from a restricted biotope (Fig. 11, p. 117) was collected for the purpose of various experiments. Yet the species was found to be still more abundant at that very place the following June. However, it must be conceded that "with the best of intentions" it might be possible to exterminate, for example, *Carabus intricatus* from Skåne.

Destruction of biotopes is far more disastrous for animals than direct collecting activity. Conversely it is much more important, where necessary, to protect by law the biotope rather than the insect.

It does not seem possible to decide whether, due to the indirect influence of mankind in recent decades, the larger number of insectivorous birds (for example, Beirne, 1947a, p. 41) has brought about a decrease in the carabid fauna. Of course Notini's study (1943, pp. 33 ff.) showed that, for instance, the hooded crow (*Corvus cornix*) feeds largely on carabids.

Much larger than the group of carabids negatively affected by mankind is the group increased as a result of human culture, with new regions for colonization and increased possibilities of dispersal.

It is obvious that among the above-mentioned 16 examples of species in process of area expansion (p. 630), no fewer than seven are markedly favored by culture. Of the 9 "late immigrants" (p. 622)—besides the probably anthropochorously transported *Clivina collaris* and *Lionychus*—this is true especially of *Amara fusca* and *Harpalus puncticeps*.

Definite promotion due to culture is enjoyed chiefly by species that show a late area expansion in the *northern* half of Fennoscandia, that is in regions where the cultural impact in the last century was most striking.

Of these species I have carried out a more detailed study of *Amara in-*
641 *genua*, which has been discussed elsewhere (pp. 525, 538). This species occurs in the north exclusively on civilized land (fields, harbors, refuse dumps, etc.). With regard to species increasing in abundance of similar habitats in Central Europe (for example, *Amara fusca*; Part I, p. 135) it was surmised that they are promoted by artificial fertilizers. However, the experiments carried out with *A. ingenua* showed that it reacts positively toward none of the generally used fertilizers. But feeding experiments with the same species revealed that it has a strong predilection for seeds and fruits of certain synanthropous plants, especially *Polygonum aviculare*. So it must be assumed that cultivated soil attracts *Amara ingenua* chiefly by virtue of the *vegetation*. It probably attracts other species too, especially of the genus *Amara*. The character of the cultivated landscape is important taking the form of oases of open grass- and meadowland in the great northern forest region. Artificial drainage of cultivated fields causes these oases to represent the only inhabitable places, often miles apart, for xerophilous and heliophilous animals.

Mention must be made of an important factor facilitating rapid dispersal of the more or less xerophilous species through the great forest regions in recent decades. I mean the construction of road and railroad networks. Soon they criss-cross the entire forest region like a blood vascular system, and their gravelly edges form endless stretches of a remarkably uniform biotope, strips of the dry meadow type. They traverse not only forest but also large bogs, offering excellent uninterrupted migration routes for all more or less xerophilous animals (and plants). Especially, railroad embankments in wooded areas are well known as rich sources of species of *Amara* and other xerophiles.

Finally it is evident that the increasingly brisk traffic, even in the northern wooded region, by rail and road has provided new possibilities of displacement, for example by transport of gravel, hay and potatoes.

3. *Area shifts are dependent on climate*. This explanation presupposes that apparent alterations in climate in most recent times can be detected.

There is already a considerable amount of literature attempting to estimate the impact of established or assumed climatic alterations on the distri-
642 bution of animals. In this field the Finnish vertebrate zoologists in particular have been very active (Siivonen and Kalela, 1937; Kalela, 1938, pp. 226 ff.; 1940a, pp. 38 ff.; 1944; 1946; 1947; 1948; Merikallio, 1946, pp. 121 ff.). Various Nordic entomologists share this viewpoint (for example, Munster, 1927, p. 289; H. Krogerus, 1945; Jansson, 1945; Valle, 1946; Ander, 1947; p. 55), in Germany chiefly Horion (1938; 1939). Earlier Ekman (1922, pp. 519–522) was skeptical of such explanations.

The above authors generally proceed from the meteorologically established fact that the *mean monthly temperatures* especially in winter and spring have gradually risen from a minimum in the middle of the last century, and that this rise (with the exception of the three years of severe winters 1940–43) has been especially strong in recent decades (Siivonen and Kalela, 1937; Hasselberg and Birkeland, 1940; Lunelund, 1942b, p. 3; Keränen, 1944; Ångstrom, 1946, p. 97, Plate V; Ahlmann, 1948; for a general viewpoint, see A. Wagner, 1940). The zoologists try to correlate these climatic changes with the increase in numbers of several heat-requiring species, and to a lesser extent with the decline of markedly northern species.

Although the monthly means reflect the general course of temperature changes over a series of years it is clear that a study of the trend of *temperature minima*—especially in spring—would be more useful from the biological viewpoint (cf. p. 467). I have collected the figures for the most important months from the Swedish State Meteorological Institute. Since measurement of minimum temperatures started in Sweden around 1880 they do not go as far back in time as the curves of the media, but they should suffice for the present purpose.

The figures considered most important (cf. p. 467) were those of the "critical" months of April, May, September, October (Lindroth, 1931, p. 480). Both, the mean and the absolute monthly minima, were taken and, for comparison, the mean temperature of each of the above months. All these figures were calculated for five-year periods and curves for the two spring months were
643 plotted after combining the values from three neighboring stations. Both the thermal effect of purely local conditions and the disturbing effect of moving the apparatus are thus rather compensated.

The diagrams (Diagram 58–61) show the following:

a. A general rise in temperature during the periods concerned is most marked in April and secondarily in May. In September the trend is utmost weak and in October imperceptible. So for the two autumn months only four stations are cited and they are ignored in the following discussion. With regard to the mean values of the above four months, the similar observations have been made in Finland (Siivonen and Kalela, 1937, p. 615; Keränen, 1944, p. 48).

b. The temperature rise of the average minima is almost always greater than that of the mean temperature of the month. This is consistently true in April and in May, especially for southern Sweden. The absolute minima are naturally distributed somewhat irregularly, but the tapering off of really low values over the last decade is distinct, especially during April.

c. The extent and general course of the recorded temperature improvement are not arbitrarily distributed all over the country. Certain parts of the country rather seem to be especially favored in this respect, in both April and May: The coastal region of northern Norrland, the inland of southern Norrland, the

Mälar and Hjälmar regions in central Sweden, and finally Gotland.

It was desirable to depict this thermal trend cartographically, since it projects very regularly in respect of the average minima of April and May. But for this, values from more stations were needed, so I preferred to prepare maps comparing the mean monthly minima of the periods 1890–99 and 1930–39 (Figs. 91, 92). Norway (after "Norske Meteorol. Inst." 1890 ff.) is also taken into consideration.

These maps show still more strikingly the regular geographical distribution
652 of climatic improvement in spring in terms of temperature minima. It is evident that, climatically speaking, this has primarily affected the continental parts of Scandinavia, whereas western Norway (probably excluding a small region in the Bergen-Sogn region* is virtually unaffected. We may be justified in taking these facts as confirmation of the supposed progressive oceanization of the Fennoscandian climate, repeatedly urged by others (Johansson, 1929; Ahlmann, 1939, p. 57; Ångström, 1939, p. 65; Hesselberg and Birkeland, 1940, p. 17, and others).

If this climatic alteration is correlated with the area shifts established or presumed above (pp. 622 ff.) for a number of carabids in Scandinavia, we seem to be justified in explaining the increase in frequency and abundance at least in part climatically (thermally) in the following cases:

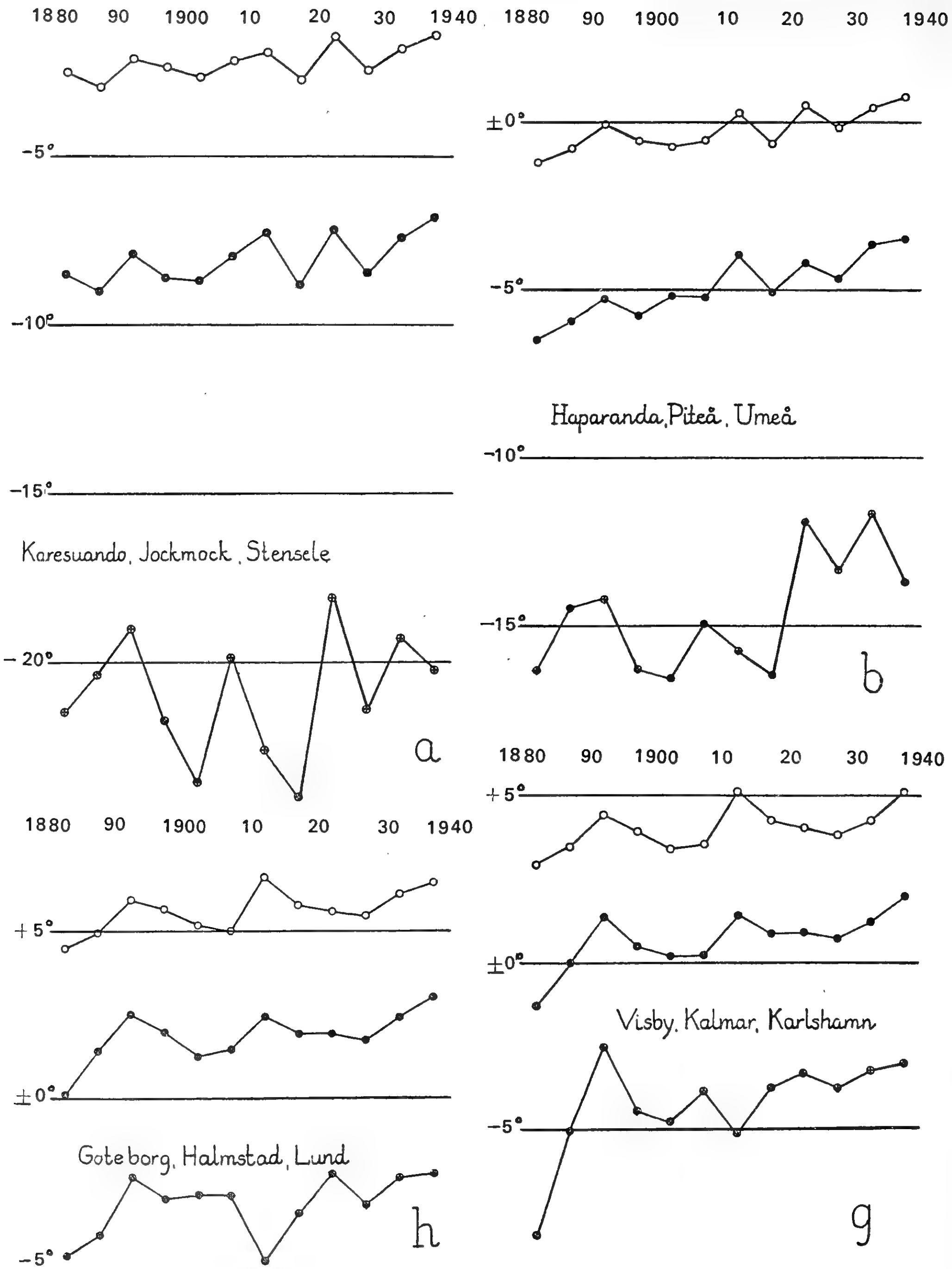
a. In eastern North Sweden. *Agonum micans*, *Amara ingenua*, *A. municipalis*, *A. similata*, *Trechus quadristriatus*. In the case of the species of *Amara*, climatic and "cultural" factors (p. 637) may have combined to exercise their effect.

b. In the central Swedish lake region. *Acupalpus exiguus*, *? Amara montivaga* (cf. Munster, 1927, p. 288), *Demetrias imperialis*, *? Odacantha melanura*, *Oodes gracilis*, *Trechus discus*.

c. On Gotland. *Harpalus rupicola*.

It is strange that the three exceptionally severe winters with their delayed spring in the years 1940–42 do not seem to have adversely affected the carabids that had immigrated or moved north in the preceding decades (cf. p. 312). The same observation was made by H. Krogerus (1945, p. 13) with respect to the lepidopteran fauna of southwestern Finland. It is possible that the shortened lifespan was compensated by the above-normal summer temperature in these three years. It is also conceivable that as soon as a species has got established in the (chiefly loco- and microclimatically) most suitable biotopes, it tolerates unfavorable macroclimatic conditions better than during the migration phase, when the individuals are exposed far more to the vagaries of nature.

*The different state of affairs in the Bergen-Sogn region is reflected in values from only two stations. It is possible that purely local conditions took effect. (In connection with the spring mean temperature, cf. Hesselberg and Birkeland, 1940, p. 18, Fig. 7, p. 23, Fig. 15.)



1880 90 1900 10 20 30 1940
−5°
−10°
−15°
Karesuando, Jockmock, Stensele
− 20°
a
1880 90 1900 10 20 30 1940
±0°
−5°
Haparanda, Piteå, Umeå
−10°
−15°
b
1880 90 1900 10 20 30 1940
+ 5°
±0°
Goteborg, Halmstad, Lund
−5°
h
1880 90 1900 10 20 30 1940
+ 5°
±0°
Visby, Kalmar, Karlshamn
−5°
g

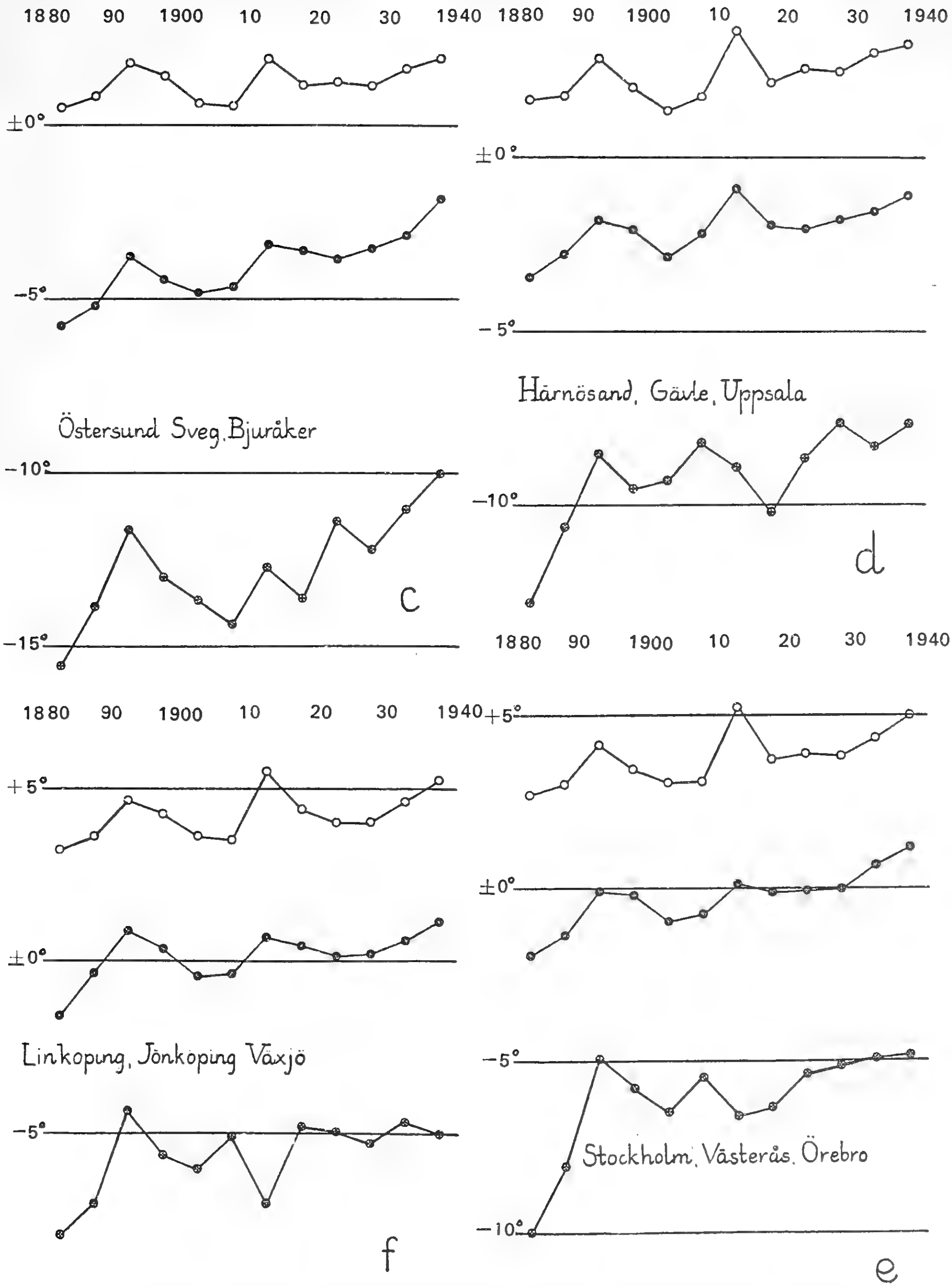
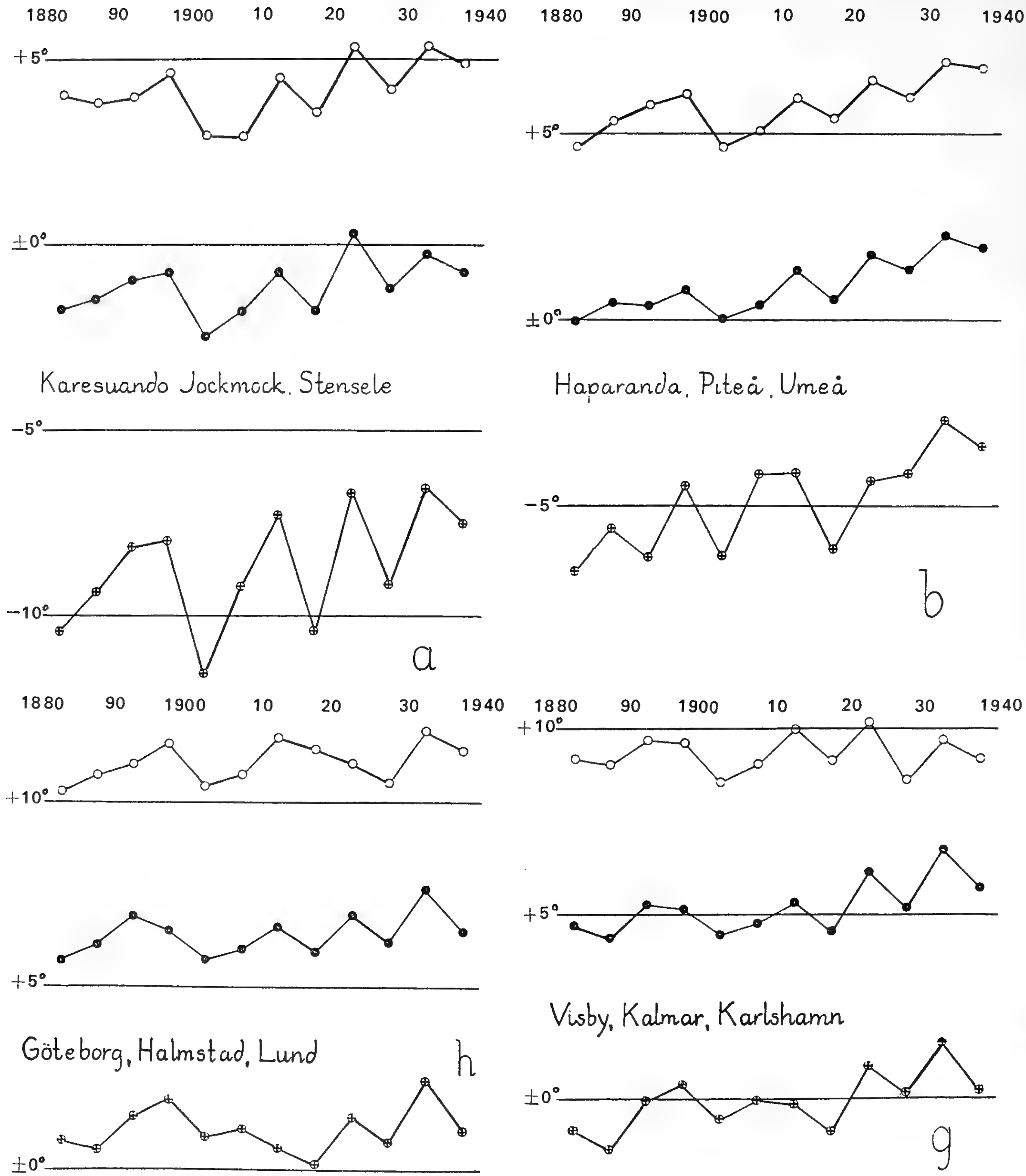


Diagram 58. April. Five-year periods in Sweden of mean temperature (Blank circles), mean daily minima (black circles) and absolute monthly minima (hatched circles). Three neighboring stations were combined in each case.


1880 90 1900 10 20 30 1940
+5°
±0°
Karesuando Jockmock. Stensele
−5°
−10°
a
1880 90 1900 10 20 30 1940
+5°
±0°
Haparanda. Piteå. Umeå
−5°
b
1880 90 1900 10 20 30 1940
+10°
+5°
Göteborg, Halmstad, Lund
h
±0°
1880 90 1900 10 20 30 1940
+10°
+5°
Visby, Kalmar, Karlshamn
±0°
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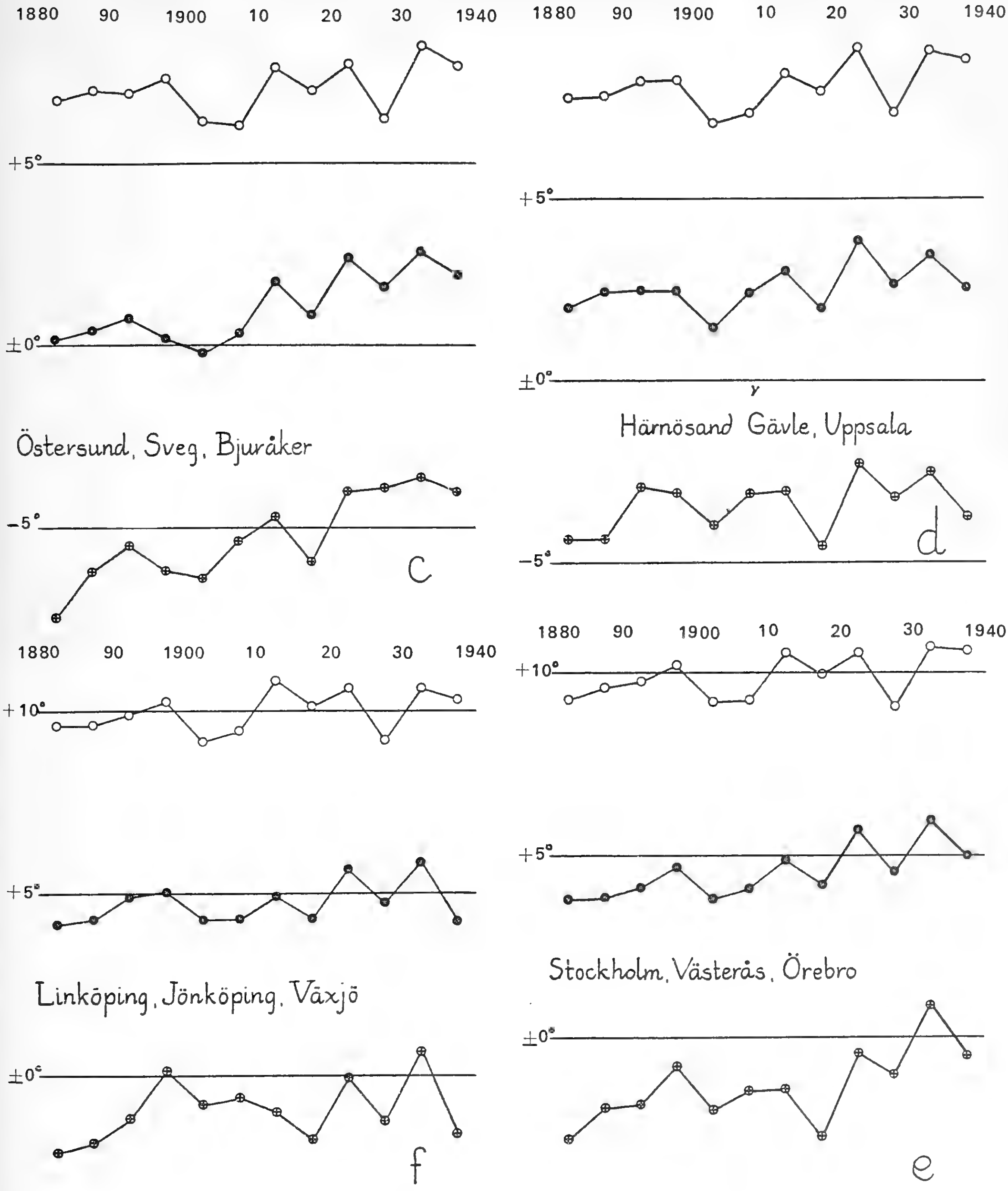
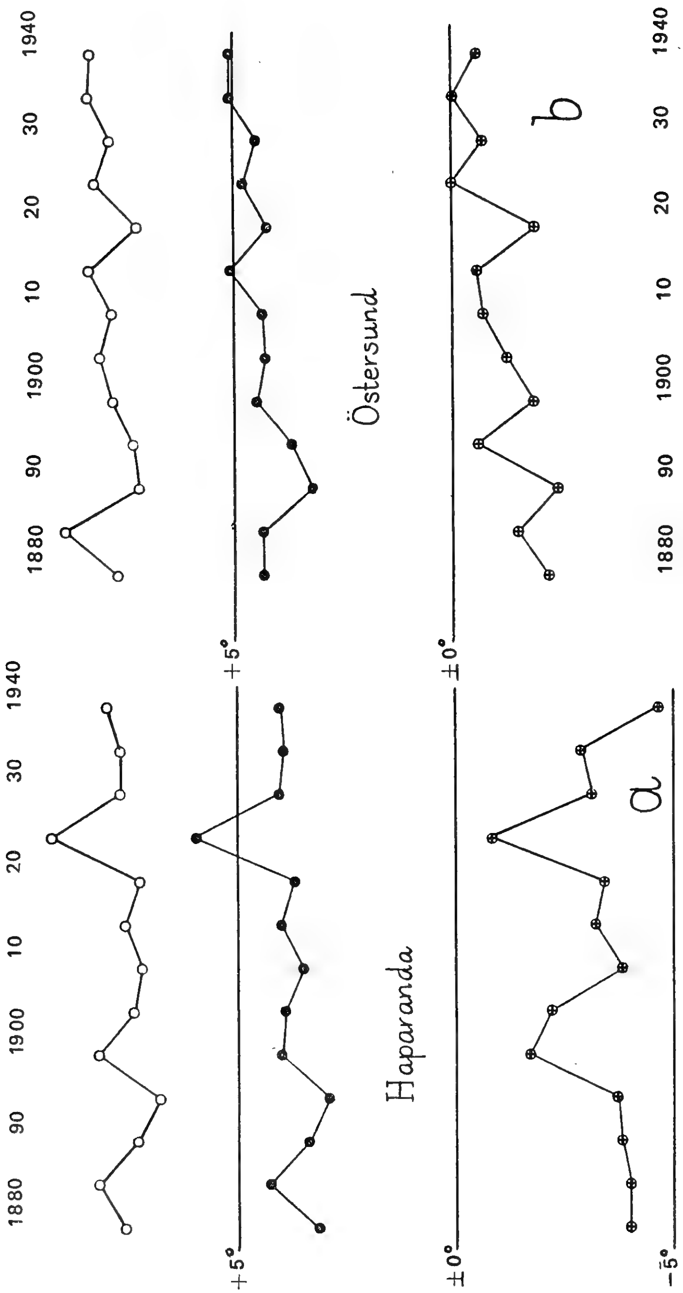
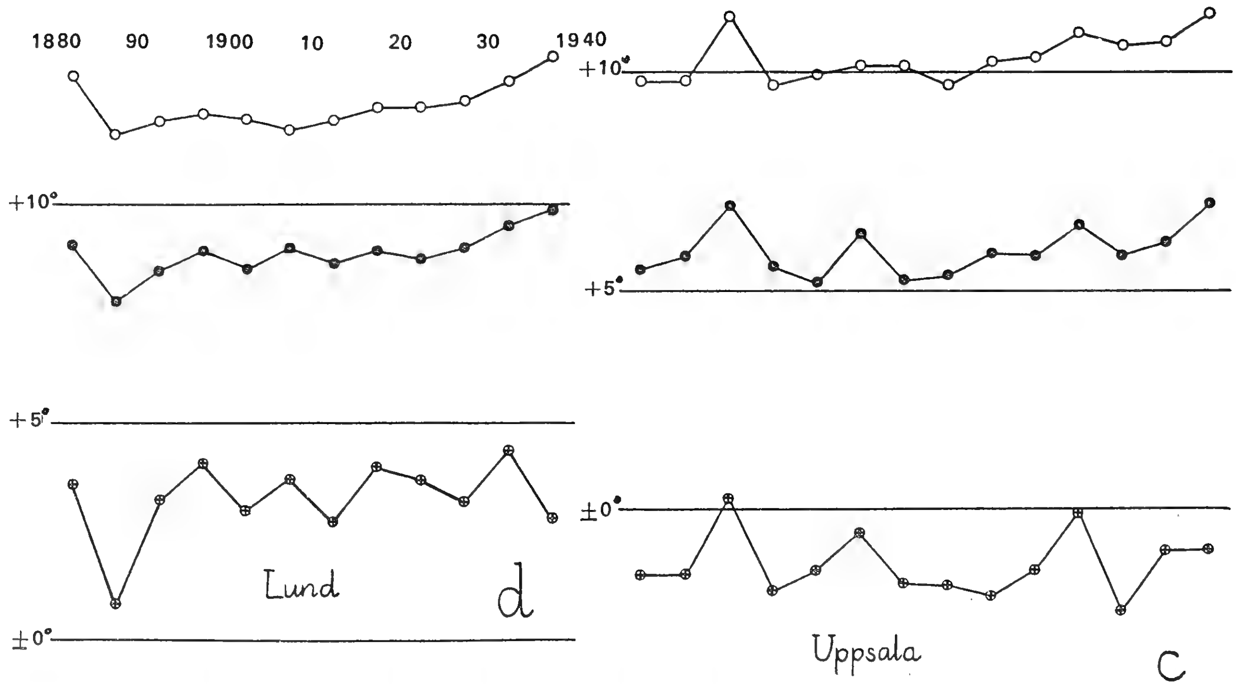
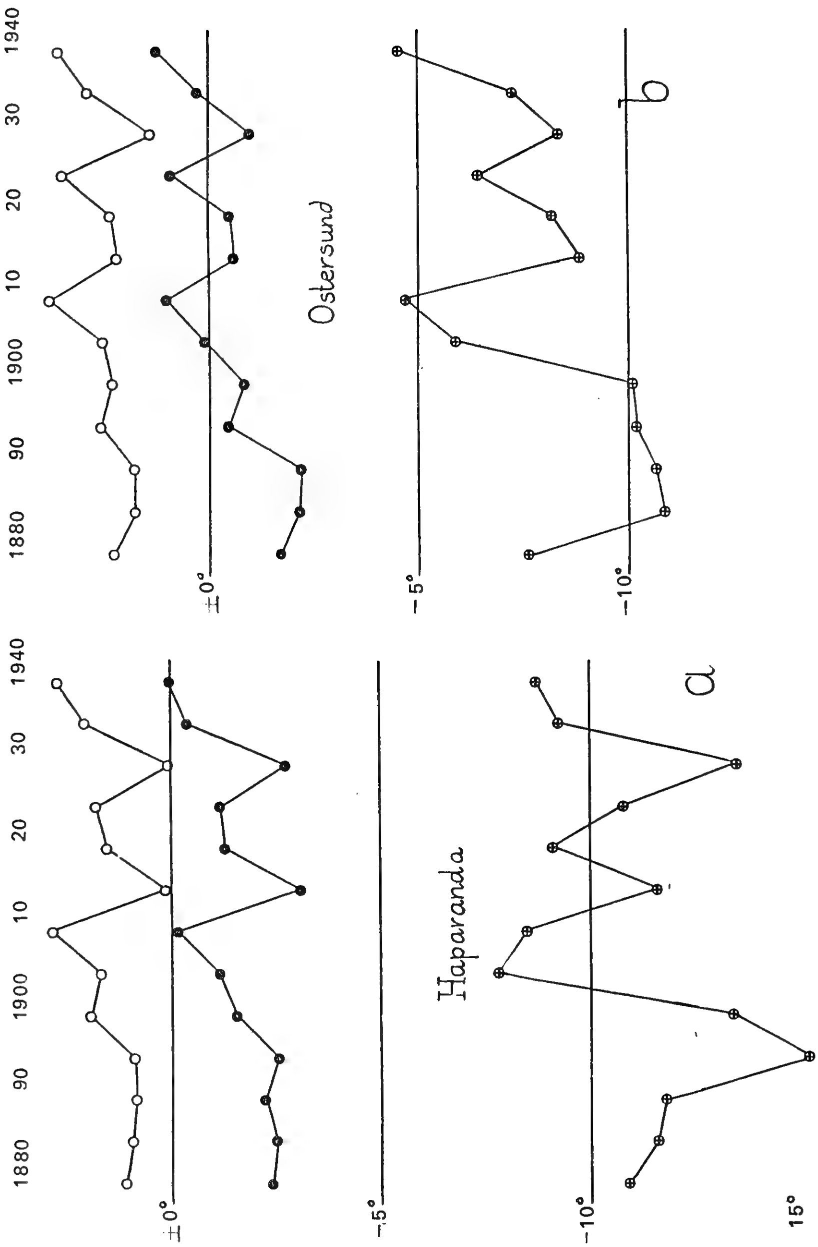


Diagram 59. May. Five-year periods in Sweden of mean temperature (blank circles), mean daily minima (black circles) and absolute monthly minima (hatched circles). Three neighboring stations were combined in each case.


Haparanda
Östersund
a
b
1880
90
1900
10
20
30
1940
+5°
±0°
−5°



648 Diagram 60. September. Five-year periods of mean temperature (Blank circles), mean daily minima (black circles) and absolute monthly minima (hatched circles) in four widely separated stations of Sweden. For explanation see Diagram 58.



1880
90
1900
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1940
±0°
−5°
−10°
Ostersund
b
1880
90
1900
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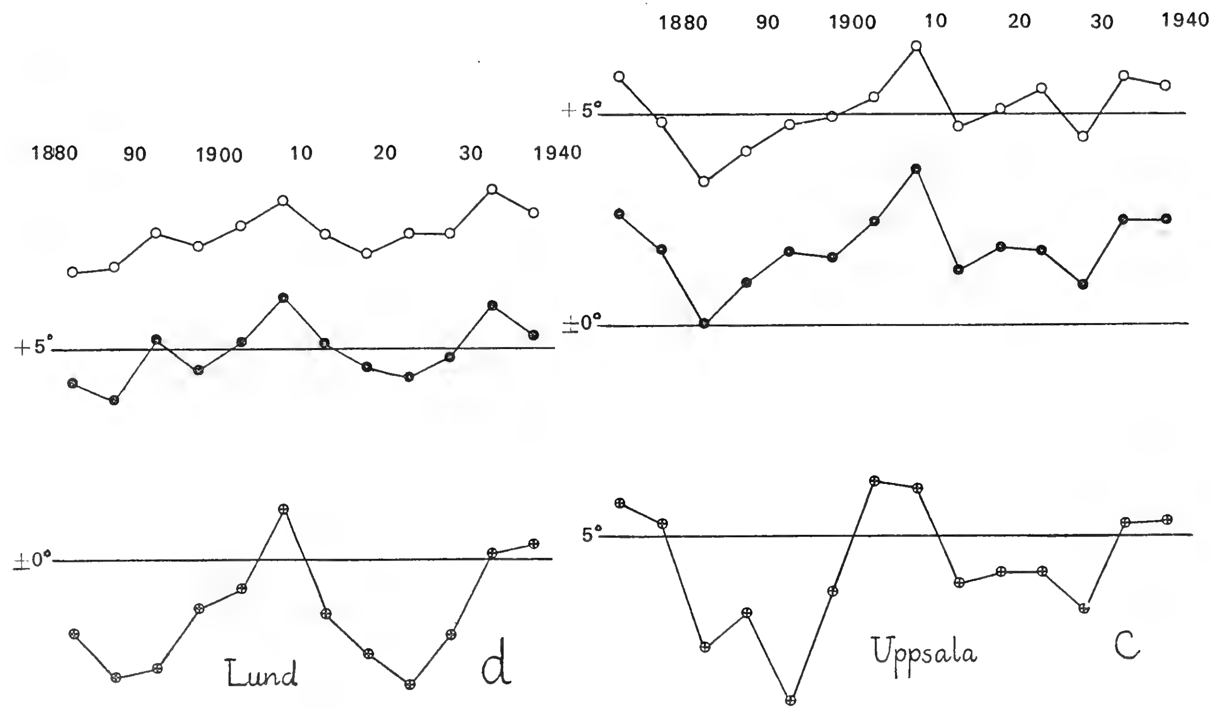
20
30
1940
±0°
−5°
−10°
15°
Haparanda
a



649 Diagram 61. October. Five-year periods of mean temperature (Blank circles), mean daily minima (black circles) and absolute monthly minima (hatched circles) in four widely separated stations of Sweden. For explanation see Diagram 58.

653 It should be emphasized that the *precipitation climate*—at any rate in Sweden—during the period (since 1860) has shown no such drastic or consequential change as the temperature climate (Bergsten, 1941; Ångström, 1941). Only in northern Sweden—especially in the fjeld regions—is a slight increase in precipitation perceptible. This manifests chiefly as an increase of about 20 days in the annual duration of snow cover. This change may have assisted the hibernation possibilities of the ground fauna.

4. *Immigration of new species into Fennoscandia depends on changes having occurred in the original species area, situated outside the region.* These alterations may be of a positive or negative nature. Of the former case an excessive population density could cause an emigration. In the latter case, emigration could be caused by destruction or deterioration of the original biotopes.

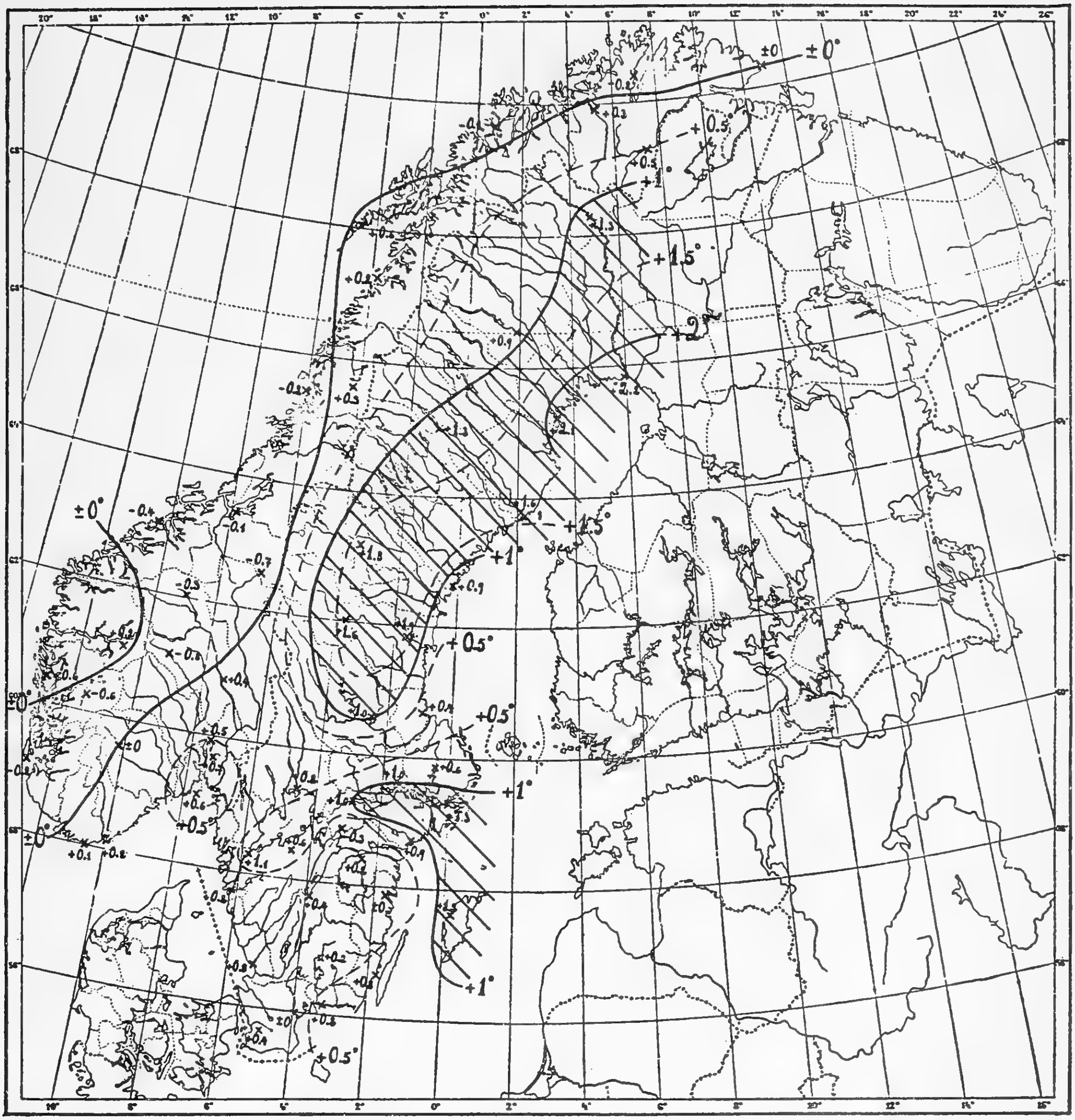
a. A hypothesis to that effect was proposed by Lönnberg (1924, pp. 112 ff.) to explain the late, rapid immigration of some aquatic birds into Sweden, chiefly of *Nyroca ferina* and *N. fuligula*. He assumes that emigration from their original homeland in West Asia followed general drying up of the lakes there. Later this hypothesis was elaborated, chiefly by Kalela (for example, 1940b; 1946, p. 35).

Among carabids there is only one species of this ecological type, *Bembidion transparens*, which is associated with vegetation-rich shores and immigrated late from the east. Of course this can apply at the most to its southern area in Fennoscandia (southern Finland, central and southern Sweden), whereas the insect must be long established in the far north, as is evident from the dimorphism map (Fig. 45, pp. 391 ff.). Possibly this interpretation also applies to the two transgrading species, *Chlaenius costulatus* and *C. sulcicollis*, which are prominent actively flying bog species. The former clearly shows its eastern origin.

Hence the "drying up hypothesis" has at best limited validity for the immigration of our carabid fauna.

654 At present it can scarcely be judged whether other unfavorable events, such as forest fires, occasional floods, cultivation of the soil, etc., taking place outside the Fennoscandian region have caused a westward or a northward migration of carabids.

b. The importance of population density for greater "dispersal urge" has been repeatedly mentioned, especially for birds and mammals (in Fennoscandia among others by Ekman, 1922, p. 517; Kalela, 1938, p. 247; 1944, p. 5). It is clear that this factor has been operative in various mass migrations of insects, for example, of *Locusta migratoria*, and among the Coleoptera, especially of various coccinellids. These examples show some animals with advanced psychic functions, for which a definite territory must be available per family for hunting or food intake. Then there are some insects which through periodic excess in numbers, and perhaps specialized food habits (coccinellids on aphids), are easily forced to emigrate as a direct result of lack of food. None of these con-



650 Fig. 91. April. Difference between mean minimum temperature of periods 1890–1899 and 1930–1939. Regions with rise of more than 1°C are hatched.

651 Fig. 92. May. Difference between mean minimum temperature of periods 1890–1899 and 1930–1939. Regions with rise of more than 1°C are hatched.

ditions applies to carabids. Mass occurrence of carabids is very rare and, as far as I am aware, a normal emigration from a region has never taken place. It must be recalled that the large number of insects washed up on the shore of seas and the larger lakes (Palmén, 1944), often very rich in carabids, results chiefly from accumulation during anemohydrochorous transportation and not from mass emigration.

The not very specialized feeding habits of carabids (p. 531) greatly reduce the effect of an accidental increase in population density. It seems improbable that the late immigration of several species to Fennoscandia can be explained by this alone.

5. *Area expansion of a species may depend on a change in its ecology*, so that new biotopes can be colonized.

Often cited as an example among Coleoptera is *Oryctes nasicornis* L. Both, in Norway (since 1905; Munster, 1927, p. 289; Natvig, in Saalas, 1939, p. 376) and in Finland (since 1919; Saalas, l.c.) it is a late immigrant. It has greatly enlarged its area in Sweden too. Originally the species was undoubtedly an inhabitant of hollows of trees, and its rapid advance north is associated with
655 its switching to "cultural" biotopes, where the beetle now generally breeds in sawdust heaps, in garden compost, etc.

Probably a similar explanation applies to the unusually vigorous invasion of *Corymbites cupreus aeruginosus* Fbr. in Finland (Saalas, 1923, 1939) since the turn of the last century. It has become a pest to cultivated grassland and cereal fields.

Among carabids there are only slight indications of such a shift to "cultural" biotopes in certain species, for example in *Harpalus distinguendus* and *H. rubripes*, *Amara nitida* and *A. montivaga*.

It is not known whether colonization of new kinds of biotopes is due to changes—hereditary or other—in the insect itself. Nobody will claim that the Colorado potato beetle (*Leptinotarsa*) must have undergone change after it shifted to *Solanum tuberosum*; it is only that contact with this plant opened up enormous new areas for colonization. Similarly ornithologists seem inclined to believe that the well-known ecological shift of the blackbird (*Turdus merula*) to cultural biotopes represents a kind of non-heritable "ecological shift" (for example, Kalela, 1944, pp. 15–17).

On the other hand, as an example of a mutation with altered ecological valence, mention may be made of the melanic form of the hamster (*Cricetus cricetus*) (Timofeeff-Ressovsky, 1940, pp. 97–99).

I still cannot decide whether pronounced "ecotypes" ("ecological mutants") also occur among the Fennoscandian carabids. The question must be investigated experimentally. Perhaps it might be worth the effort to study in this connection species like *Demetrias monostigma*, *Dromius longiceps* and *D. sigma*, which are characterized by a peculiar "double ecological occurrence" (see Part I).

This does not mean that any of the late immigrants among the Fennoscandian carabids had to emigrate from its original homeland on account of changed ecological requirements, except perhaps *Amara majuscula*?

In conclusion the following two most important causes of recent changes in the Fennoscandian carabid fauna may be established:

656 1. Alteration of the landscape due to civilization, partly associated with anthropochorous dispersal.

2. Thermal climatic improvement, especially of the spring minima, over recent decades.

However, sudden invasions of large numbers, such as those by *Amara majuscula*, which in many respects remind us of the immigration of the geometrid *Eupithecia sinuosaria* Ev. (Wahlgren, 1921), remain enigmatic. In these cases it is difficult to avoid the conjecture that a physiological alteration of the insect itself must have taken place.

The persistent impression of the present section is undoubtedly that of pronounced lability on the part of the Fennoscandian fauna. During the geologically insignificant period of one century, considerable faunal alterations have taken place. One must then ask if it is actually possible to assess, even approximately, faunistic events over the entire postglacial period of which the period considered here constitutes less than 1%, not to mention events even farther back in time. Yet how far the attempt is justified will be evident from the subsequent sections. Nevertheless, it can be safely argued that the last 100 years, chiefly because of drastic influence of civilization, have been the most fateful of the entire postglacial period for fauna and flora.

Fossil Records

Reconstruction of the postglacial—and older—history of the fauna is possible through the study of fossil and subfossil animals and of the peculiarities of the present-day distribution of each species. The latter method involves much speculation and must be pursued with caution. On the other hand, fossils (including subfossils) provide exact evidence of the faunal conditions of a particular period in a particular region. Uncertainties are, first, age determination—in which today's refined pollen analysis is a valuable aid—and, second, the difficulty of correctly identifying a more or less reduced, often postmortally altered
657 animal fragment. I have recently (Lindroth, 1948a) considered this last question and shown that in fossil carabids both the corrugation of the chitin and the formation of more or less regular dots (especially on the intervening spaces of the elytra) may occur as a result of postmortem changes. But the study of microsculpture is often the only certain way to determine a fossil carabid fragment. For instance, the elytra of the subgenus *Europhilus* (*Agonum*) can be separated only in this way. The standard rule for the identification of a fossil must be: Only specimens that are recognizable with complete certainty should

be given a name: new descriptions of "extinct" species should be provided only in unambiguous cases. One must always bear in mind that wrong determination of a fossil can have far worse consequences than that of a recent animal.

The study of subfossil insects has been neglected in Fennoscandia, especially because the peat geologists have almost ignored it. The best studied is the Quaternary subfossil fauna of Skåne (and Denmark), which was worked out comprehensively by Henriksen (1933). His determinations seem to be thoroughly reliable, and I have only in exceptional cases found it necessary to check his records. However, he has included some of the older records from Skåne only from the literature (G. Andersson, 1889; Holst, 1906, 1908, 1911; Kurck, 1917; Kolbe, 1933), and undoubtedly it would be desirable to check some of the determinations. Unfortunately, it was impossible to locate the material in question in any museum, and the records from Skåne are given in responsibility of the original author.

From the rest of Sweden there are only a few records on subfossil carabids in the literature, and the interglacial material that I recently worked out (Lindroth, 1948a). Later I obtained various postglacial subfossils from different sources (ML, PU, SG; for abbreviations see below), chiefly from the "warm period."† These records are included in the catalog below.

It is lamentable that (in PU) of the "remains of beetles" collected in a thorough investigation of the peat bogs of Norrland by Post (1906), very few
658 could be traced. With their precise dating they would have been especially interesting.

The enormous quantities of peat samples of SG could certainly reveal various subfossils of insects. With regret I have had to forgo this time-consuming work. Perhaps some young Swedish entomologist will devote himself to this fascinating field before too long.

In addition to solitary finds, material from two rich Swedish subfossil localities was available to me. These findings deserve to be briefly described:

a. Vgl Vårgårda, Lärke-mosse (Bengt Ekengren). The beetle remains were at a depth of 90 to 110 cm. Two peat samples at this level were kindly subjected to pollen analysis by Dr. Gösta Lundqvist (Sveriges Geol. Undersökn.) and were provisionally dated to the Bronze Age (possibly the earlier part, the Sub-boreal). More definite determination is not possible without a complete series of samples. At any rate, deposition must have taken place before the subatlantic climatic deterioration. Among the carabids, *Calosoma inquisitor*, *Carabus coriaceus* and *C. cancellatus* were present. The material belongs to the Zoological Institute, Lund.

b. Dlr Stora-Tuna, Skärsjö (E. Bergquist). The subfossils were located in a peat bog at various depths and a precise dating of each stratum remains to be

†(cf. p. 687; suppl. scient. edit.)

done. But it is indubitable that all the insect remains originate from the "warm period" (probably chiefly from the late atlantic period), so are older than the subatlantic period. Hazelnuts were abundantly represented in the deposits. A complete pollen analytical series through the entire peat profile was worked out by Gösta Lundqvist. Ten species of carabids were represented (see list below), of which *Carabus arvensis* and *C. coriaceus* are most interesting. The material belongs to "Sveriges Geol. Undersökn.", Stockholm.

Also noteworthy are the subfossil records made by Samuelsson at two places in central Dalarna (Älvdalen, Lokbodarne; Evertsberg). He has precisely dated them, though not on the basis of pollen analysis. These findings have been utilized from the botanical viewpoint in a separate publication (Samuelsson, 1906). Of special interest is the occurrence of *Trechus rivularis* in the atlantic period. The material belongs to the Paleontological Institute, Uppsala.

659 From Finland, Poppius (1911) determined and published the subfossil beetles in a number of postglacial peat samples collected by Harald Lindberg. Unfortunately I obtained only part of this material for examination, and these subfossils, which were rediscovered in the Helsinki Museum, lacked determination labels by Poppius. However, since he lists the insect remains found in each stratum along with a precise description of the various profiles of the deposit, it is generally possible to decide which subfossil he had before him in each case when he named them. Revision—to the extent that the material could be traced—revealed the following:

St. Kiukais, Panelia (PPP 1911, pp. 9, 38). *Agonum* cfr. *gracile*, 1 elytron = *A. thoreyi.*

Ik Metsäpirtti, Viisjoki (pp. 17, 36–38). *Calathus micropterus* is missing from this locality; however, there is an elytron of the same species bearing the label "Valkjärvi Siipsuo."

Amara cfr. *acuminata*, 1 damaged elytron = *Pterostichus* sp.

Agonum dolens, 1 very poorly preserved elytron, probably = *Europhilus* sp.

Ik Rautu, Osmina (pp. 18, 37–38). *Pterostichus diligens*, 1 elytron = *P. nigrita.*

Agonum cfr. *gracile*, several elytra = *A. fuliginosum* 1 specimen, *Patrobus assimilis* 1 specimen, *Pterostichus ? diligens* 1 specimen.

Ik Rautu, Osmina (pp. 18, 37–38). *Agonum* cfr. *gracile*, 2 records, 1 poorly preserved elytron = ? *Europhilus* sp.

A. viduum 2 elytra, poorly preserved = ? *Agonum* sp.

Trichocellus placidus, 1 elytron, poorly preserved = *Pterostichus* sp.

Ik Sakkola, Isosuo (pp. 22–24, 36–38). *Agonum* cfr. *gracile*, 1 elytron = *Europhilus* sp.

Pterostichus diligens, 1 elytron = *Pterostichus ? diligens.*

Oodes helopioides, 1 elytron = *Oodes helopioides.*

Oa Ilmola (p. 38). *Agonum* cfr. *gracile*, 1 elytron = *Agonum gracile*.

It is regrettable that in the Helsinki Museum no record material was to
660 be had for the three species *Bembidion grapei*, *Pterostichus vermiculosus* and *P. ? archangelicus* Popp. found in the late glacial deposits from Ik Kivennapa (PPP. 1911, pp. 16, 36–37). At any rate the determination of the *Bembidion* species is to be considered very uncertain. The highly characteristic *Pterostichus vermiculosus* could hardly have been mistaken.

On the whole the determination of subfossils by Poppius does not give the impression of being reliable and generally cannot be accepted without verification. Finnish entomologists who have observed his identification work tell me that it was hasty and superficial.

Recently, A.L. Backman has diligently assembled extensive subfossil beetle material, especially from Österbotten, which is now preserved in MH. I studied the Carabidae material. Unfortunately it was possible to obtain precise information, especially on age, only for part of these records, but all of them are postglacial. The records are incorporated in the list below.

In the first "special" part of this book the then known subfossil records were given along with each species. Since then considerable contributions have been added. Also I overlooked some of those in the literature. For these reasons, and for greater clarity, it is advisable here to give a complete list of records of subfossil carabids in Fennoscandia. Denmark, whose postglacial history largely tallies with that of Skåne, is included. Subfossil records from other regions have not been included. For them, reference may be made to Part I of this book and to the Supplement at the end of this part.

As far as possible, along with each species an indication of the time period is given according to the usual scheme of late and postglacial periods (Table 36). There is no consensus among Quaternary geologists, so this scheme is partly a compromise among different opinions (Högbom and Lundqvist, 1930, p. 157; Gross, 1930, p. 94; Nordhagen, 1933; Henriksen, 1933, p. 92; Wagner, 1940, p. 128; Sandegren and Asklund, 1946, p. 96). Dissenting opinions, especially with regard to the Ancylus period, have been expressed by Munthe (1940, p. 63, etc.) and Sauramo (1942, pp. 232 ff.).

663 It would be incorrect to introduce, with Henriksen (l.c.), the hypothetical mean July temperature of the different periods (following A.C. Johansen, 1906; Johansen and Lynge, 1917; according to this the maximum temperature in the sub-boreal). There are still no reliable methods of determining such figures, even approximately. It is also rather audacious to shift the postglacial temperature maximum already to the later part of the Boreal period (Gross, 1930, p. 95; Wagner, 1940, p. 129, puts it still farther back, around about 7000 B.C.). But it gives an idea—certainly correct in principle—of the steep temperature rise at the end of the late-glacial period (before the bipartition of ice in Jämtland). On the other hand, according to Sauramo (1942, p. 263) the thermal optimum set in during the first half, according to v. Post (1924,

p. 114) and Granlund (1932, p. 169) in the later half of the atlantic period; also in Denmark during the Atlanticum (Iversen, 1941, p. 38). The "warm period" certainly extended into the sub-boreal; during this period, the maximum of *Trapa natans* occurred in Sweden (Samuelsson, 1934, p. 194; see also Sernander, 1908, pp. 213 ff., and the *Trapa* map by Jessen and Milthers, 1928, p. 349).

664 In the checklist below the following abbreviations are used:

For authors

BCM—A.L. Backman
HNR—K.L. Henriksen
LBH—Harald Lindberg
LTH—C.H. Lindroth
PPP—B. Poppius.

For institutions

GH—Geological Research Institute, Helsinki.
GL—Geological Institute of the University, Lund.
MC—Zoological Museum, Copenhagen.
MH—Zoological Museum of the University, Helsinki.
ML—Zoological Museum of the University, Lund.
PU—Paleontological Institute of the University, Uppsala.
SG—Sveriges Geolog Undersökning (Swedish Geological Survey), Stockholm.

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Abax ater

Denmark. Sjælland, Femsølyng-Mose, subatlantic (HNR, 1933, p. 140).

Agonum consimile

Sweden. Ång Långsele, (Riss-Würm-) interglacial (LTH, 1948a, p. 11).

Agonum dolens

? *Finland.* Ik Metsäpirtti, late postglacial (PPP, 1911, pp. 17, 38); probably wrongly determined (see p. 659).

Denmark. Sjælland, Vintappermosen, late glacial (HNR, 1933, p. 130).

Agonum ericeti

Denmark. Sjælland, Femsølyng-Mose, subatlantic (HNR, 1933, p. 130).

661 **Table 36. Outline of late-glacial and postglacial development of northern Europe.**

Compiled from Högbom and Lundqvist, 1930; Gross, 1930; Henriksen, 1933; Nordhagen, 1933; Lindqvist, 1935 (p. 51); Munthe, 1940; Wagner, 1940; Sauramo, 1942; Sandegren and Asklund, 1946

	Ice edge	Baltic Sea	Climate		Culture	
A.C. 1950					Historical period	1950
1000				Subatlantic (generally moist)	Iron age	1000
0		Present-day Baltic Sea	Deterioration of climate			0
B.C. 1000					Bronze Age	1000
2000				Sub-boreal (generally dry)		2000
3000		Littorina Sea			Late Stone Age	3000
4000				Atlantic (generally moist)		4000
5000			Warm period		Early Stone Age	5000
6000				Boreal (generally dry)		6000
7000	Bipartition in Jämtland	Ancylus Lake	Warm Maximum ?		First men in Sweden ?	7000
8000	Stockholm region	Yoldia Sea		Subarctic		8000
9000	Vgl. Billingen					9000
10000		Baltic Ice Lake				10000
11000				Arctic		11000
12000						12000
13000						13000
B.C. 14000	Southcoast of Skåne					14000

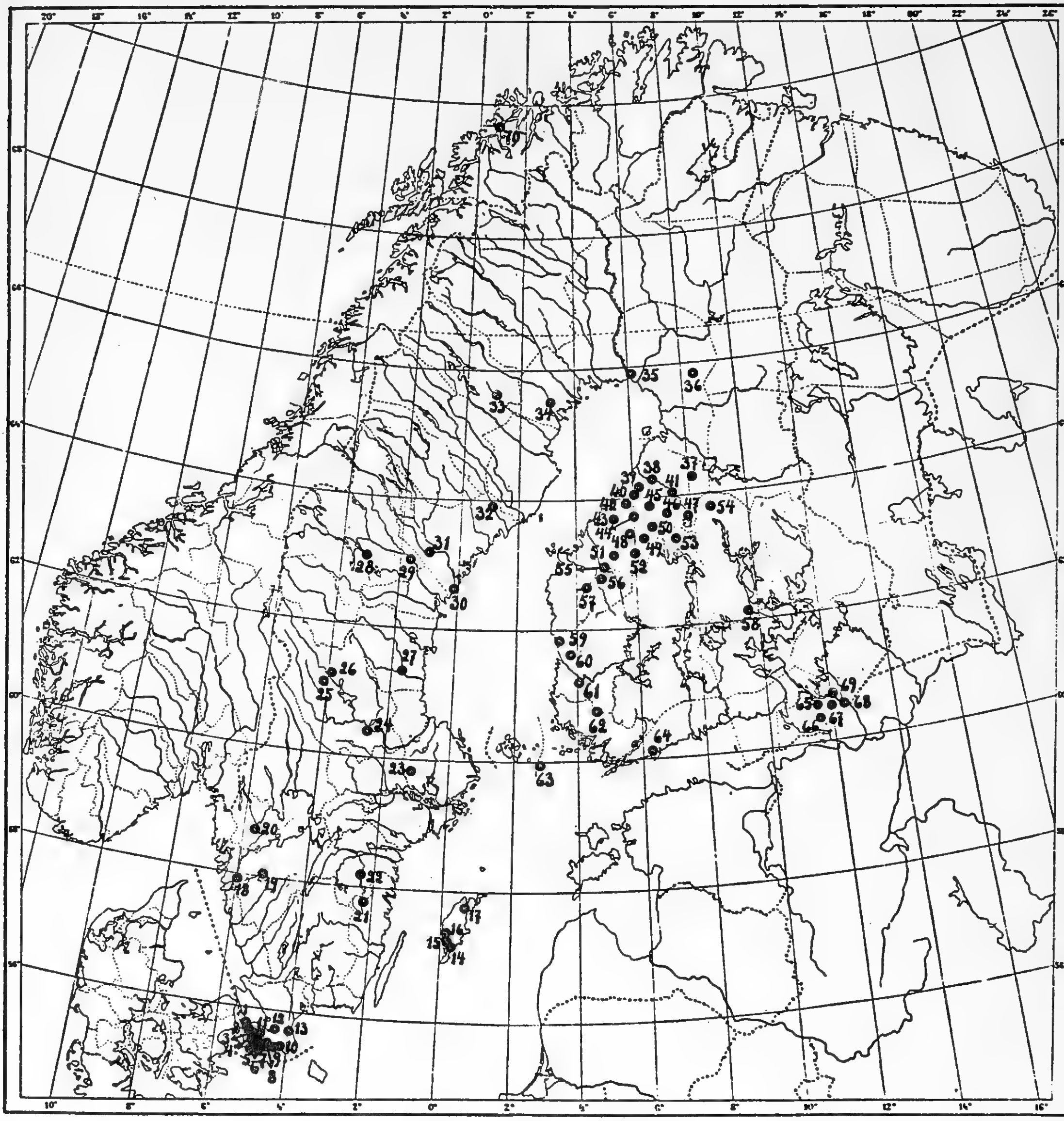

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Fig. 93. Fennoscandian localities of subfossil Carabidae.

Sweden: 1—Skå Löddesborg; 2—Åkarp; 3—Bara and Nevishög; 4—Skå Svedala; 5—Trälleborg; 6—Lindved; 7—Önnarp; 8-Skå Skurup; 9—Snårestad, Sjörup, and V. Nöbbelöv; 10—Öja; 11—Skå Toppeladugård; 12—Bjärsjölagård; 13—Brösarp; 14—Gtl Havdhem; 15—Sproge; 16—Fröjel; 17—Lärbro;

Agonum fuliginosum

Sweden. Ång Långsele, (Riss-Würm-) interglacial (LTH, 1948a, p. 11). Skå Lindved, boreal (HNR, 1933, p. 133). Dlr Evertsberg, in sub-boreal *Sphagnum* peat, elytron without apex (G. Samuelsson, PU!); Stora-Tuna Skärsjö, "Warm period", 3 elytra (E. Bergquist, SG!). Nbt Piteå, Borgsfors, probably sub-boreal, 1 elytron (G. Nordwall, MH!).

Finland. Tb Pihtipudas, Alvajärvi Lake, atlantic or early sub-boreal, 1 elytron (BCM, MH!). Ab Pöytyä, Pinomaesuo, sub-boreal, 1 elytran (GH!). Om Lappäjärvi, Kärnä, Littorina, 4 elytra (BCM, MH!). Ob Alatornio, post-Littorina, 1 elytron (BCM, MH!). Om Rautio, Kärkiskylä, postglacial, 1 elytron (BCM, MH!); Alavieska, Koiraneva, postglacial, 1 elytron (BCM, MH!); Nedervetil, postglacial, 1 elytron (BCM, MH!); Perho, postglacial, 1 elytron (BCM, MH!). Ik Rautu. Osmina, late postglacial, 1 elytron (LBH, MH!). The doubtful record from Nl Ingå, late postglacial (PPP, 1911, pp. 11, 38), is very uncertain.

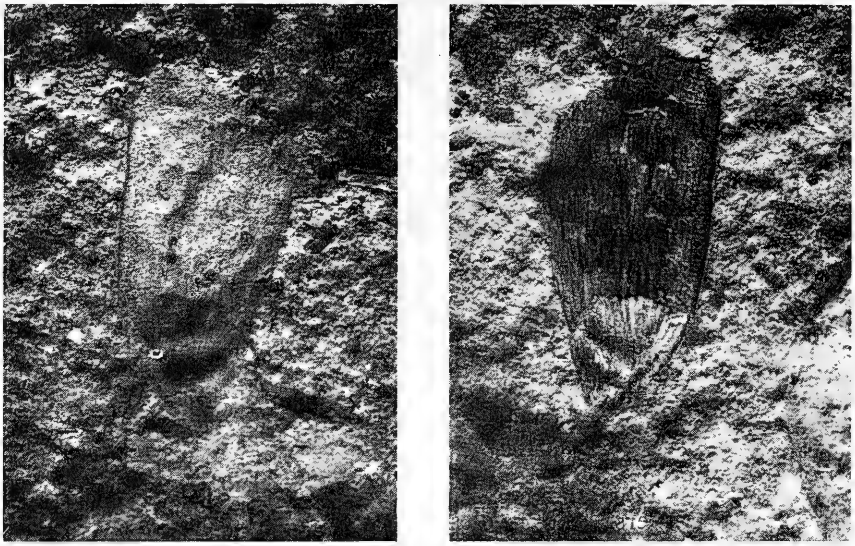
Denmark. Jutland, Esbjerg, late-glacial; Skagen, "Warm period" (HNR, 1933, p. 133).

Agonum gracile

Sweden. Skå Skurup, Saritslöv, "Warm period" (Kurck, 1917, p. 52; HNR, 1933, p. 132).

Finland. Om Haapajärvi, Haga, atlantic, 1 elytron (BCM, MH!). Sb. Vieremä, Kallolampi, Littorina, 1 elytron (BCM, MH!). Om Alavieska, Koiraneva, and Keinola, postglacial, 1 elytron each (BCM, MH!); Oulais, Hirvineva, postglacial, 1 elytron (BCM, MH!). Oa Ilmola, postglacial, 1 elytron (PPP, 1911, p. 38; MH !). The records of "*Agonum* cfr. *gracile*" from various postglacial peat deposits of South Finland by Poppius (1911, p. 38) are to be disregarded (with the exception of Oa Ilmola).

18—Vgl No 1; 19—Vårgårda; 20—Dsl Mellerud; 21—Små Djursdala; 22—Ögl Järnlunden; 23—Upl Vittinge; 24—Dlr Stora Tuna; 25—Evertsberg; 26—Lokbodarne; 27—Hls Bollnäs; 28—Jtl Pilgrimstad; 29—Ragunda; 30—Ång Härnön; 31—Långsele; 32—Bjurholm; 33—Pil Arvidsjaur 34—Nbt Borgfors; **Finland**: 35—Ob Alatornio; 36—Ranua; 37—Om Pelso; 38—Oulais; 39—Alavieska; 40—Rautio; 41—Haapavesi; 42—Kannus; 43—Nedervetil; 44—Toholampi; 45—Sievi; 46—Haapajärvi; 47—Pyhäjarvi; 48—Kaustinen; 49—Reisjärvi; 50—Kärsämäki; 51—Lappajärvi; 52—Om Perho; 53—Tb Pihtipudas; 54—Sb Vieremä; 55—Oa Lapua; 56—Nurmo; 57—Ilmola; 58—Sb Jorois; 59—St Merikarvio; 60—Pomarkku; 61—Kinkais; 62—Ab Pöytyä; 63—Al Kökar; 64—Nl Kyrkslätt; 65—Ik Valkjärvi; 66—Kivennapa; 67—Rautu; 68—Metsäpirtti; 69—Sakkola; **Norway:** 70—35 Tromsö.



664 Fig. 94. *Calosoma sycophanta* in Ancylus clay, Upl Vittinge, Skattmansö. Right elytron (right) and its impression (left). (Photo: C. Larsson).

Agonum lugens

Denmark. Jutland, Herning (Riss-Würm-) interglacial (HNR, 1933, pp. 131, 286).

Agonum micans

666 *Sweden.* Skå Skurup, Kallsjö, "Warm period," (HNR, 1933, p. 132).
The determination is probably correct (MC!).

Agonum ? moestum

Denmark. Jutland (Riss-Würm-) interglacial (HNR, 1933, pp. 131, 286). The determination is to be considered uncertain. The record from Sweden by Mjöberg (1916, p. 7) is erroneous (LTH, 1948a, p. 5).

Agonum mülleri

Denmark. Jutland, Kandestederne, "Warm period" (HNR, 1933, p. 130).

Agonum piceum

Finland. Om Pelso, early Atlantic, "Warmth flora," 1 elytron; Kärsämäki, Kintasahonräme, and Kärsämenneva, early atlantic, "Warmth

flora," respectively 5 and 1 elytra; Pyhäjärvi, Hoikkaneva, early postglacial, 1 elytron. Ob Alatornio, early postglacial 1 elytron. Om Rautio, Kärkiskylä, postglacial, 1 elytron; Reisjärvi, postglacial, 1 elytron; Alavieska, Koiraneva, postglacial, 1 elytron; Haapavesi, Piipsanneva, postglacial, 1 elytron. St. Merikarvia, postglacial, 1 elytron. (All BCM, MH!). The late postglacial record from Oa Ilmola (G. Andersson, 1898, p. 143) was doubtfully determined.

Denmark. Jutland, 2 localities, one of these records from the "Warm period" (HNR, 1933, p. 132).

Agonum thoreyi
(see map in Fig. 95, p. 675)

Finland. Om Lappajärvi, Kärnä, Littorina, 2 elytra. Ob Alatornio, late Littorina (hence probably sub-boreal). 1 elytron, Om Alavieska, Kotaräme, probably sub-boreal, 1 elytron; Alavieska, Keinola, postglacial, 1 elytron; Rautio, Kärkiskylä, postglacial, 1 elytron; Kaustinen, postglacial, 1 elytron (all BCM, MH!). Oa Nurmo, Paukaneva, sub-boreal, 1 elytron (GH!). St. Kiukais, Panelia, late postglacial (see PPP, 1911, pp. 6 ff.), 1 elytron (LBH, MH!). St. Pomarkku, very fresh elytra of 2 specimens (GH!).

Denmark. Sjælland, Femsølyng-Mose, "Warm period" (HNR, 1933, p. 133).

Agonum viduum

Sweden. Skå Toppeladugård, late-glacial (Holst, 1906, p. 8; HNR, 1933, p. 131). The determination would require verification.

Finland. Ik Sakkola, late postglacial (PPP, 1911, p. 39); determination uncertain (see p. 659).

Amara alpina

Sweden. Ång Härnön; Ång Långsele; Jtl Pilgrimstad; (Riss-Würm-) interglacial (LTH, 1948a, p. 10). Skå Snårestad, late-glacial (G. Andersson, 1889, p. 30; HNR, 1933, p. 140).

Denmark. Jutland, Martørv-Bakker, late-glacial (HNR, l.c.).

Amara bifrons

Sweden. Gtl Sproge, Snoder, Littorina period, 1 elytron (v. Post, 1903, p. 356, "*Anchomenus* sp.", PU!).

667 *Amara quenseli*

Sweden. Skå Trälleborg, late-glacial (HNR, 1933, p. 166).

Bembidion ? glaciale Heer

Sweden. Skå Svedala, late-glacial (HNR, 1933, p. 128; MC!). Today missing from the whole of northern Europe. I have examined the elytron (apex lacking) and will not venture to confirm the identification. The strongly developed 7th band is strange, but too little material of this variable species was available to me. At any rate this species is no longer found in Fennoscandia.

Bembidion ? grapei

Finland. Ik Kivennapa, Linnamäki, late-glacial (PPP, 1911, pp. 16, 36). The determination is very uncertain.

Bembidion hasti

Sweden. Jtl Pilgrimstad, (Riss-Würm-) interglacial (LTH, 1948a, p. 9). Skå Bara, late-glacial (HNR, 1933, p. 128; MC!).

Bembidion prasinum

Sweden. Jtl Pilgrimstad, (Riss-Würm-) interglacial (LTH, 1948a, p. 8).

Bembidion quadrimaculatum

Denmark. Sjælland, Femsølyng-Mose, "Warm period" (HNR, p. 128).

Bembidion repandum

Denmark. Sjælland, Knabstrup, late-glacial (HNR, 1933, p. 127, "*femoratum*"). The well-preserved elytron shows the microsculpture very characteristic of *repandum* (MC!).

Bembidion stephensi

Denmark. Jutland, Skagen, "Warm period" (HNR, 1933, p. 127, "*ruficorne*").

Blethisa multipunctata

Sweden. Gtl Sproge, Snoder, Littorina period, head and prothorax (v Post, 1903, p. 356, "*Feronia* sp.", PU!).
Finland. Nl Kyrkslätt, late postglacial (PPP, 1911, pp. 13, 36).

Calathus fuscipes

Denmark. Jutland, Egtved, "Warm period" (HNR, 1933, p. 129).

Calathus melanocephalus

Norway. Tromsö, undetermined age, 1 elytron (MT!).

Calathus micropterus

Sweden. Dlr Evertsberg, sub-boreal-atlantic 2 elytra (G. Samuelsson, PU!).
Finland. Om Lapparjärvi, Kärnä, Littorina, 1 elytron (BCM, MH!). Ik Metsäpirtti, Viisjoki, postglacial (PPP, 1911, pp. 17, 38); Valkjärvi, Siipsuo, postglacial, 1 elytron (Har. Lindberg, MH!).

668 *Calosoma inquisitor*

Sweden. Skå Skurup, boreal (HNR, 1933, p. 123). Vgl Värgärda, Lärke-mosse, sub-boreal, thorax, both elytra, etc. (B. Ekengren, ML!).

Calosoma sycophanta

Sweden. Upl Vittinge, Skattmansö, Ancylus clay (boreal) 1 complete elytron (Fig. 94, PU!). Vgl Nol, atlantic, Dsl Mellerud, probably likewise "Warm period" (LTH, 1942b).

Carabus arvensis

Sweden. Dlr Stora-Tuna, Skärsjö, "Warm period," anterior half of an elytron (E. Bergquist, SG!).

Carabus cancellatus

Sweden. Vgl Vårgårda, Lärke-mosse, sub-boreal, 1 elytron without apex (B. Ekengren, ML!).

Carabus coriaceus

Sweden. Dlr Stora-Tuna, Skårsjö, "Warm period" (apparently late atlantic), abdomen and both elytra (E. Bergquist, SG!). Vgl Vårgårda, Lärke-mosse, sub-boreal, 2 fused elytra and various other parts of the body (B. Ekengren, ML !).

Carabus glabratus

Sweden. Skå Sjörup, Bräkna-mosse, boreal (G. Andersson, 1889, p. 24; HNR, 1933, p. 124). Dlr Stora-Tuna, Skärsjö, "Warm period," parts of thorax and 2 elytra (E. Bergquist, SG !).
Denmark. Sjaelland, Femsølyng-Mose, subatlantic (HNR, 1933, p. 124).

Carabus granulatus

Sweden. Skå Skurup, Sandåkra, "Warm period" (HNR, 1933, p. 124). Gtl Lärbro, early postglacial (Sernander, 1894a, p. 64).

Carabus hortensis

Denmark. Sjælland, Femsølyng-Mose, both from the "Warm period" and subatlantic (HNR, 1933, p. 124).

Carabus nitens

Denmark. Sjælland, Femsølyng-Mose, "Warm period" (HNR, 1933, p. 123).

Carabus violaceus

Sweden. Dlr Stora-Tuna, Skarsjö, "Warm period," well preserved remains of at least 4 specimens (E. Bergquist, SG!).

Denmark. Sjælland, Femsølyng-Mose, both from the "Warm period" and subatlantic (HNR, 1933, p. 123).

Chlaenius costulatus

Sweden. Skå Toppeladugård, late-glacial (Holst, 1906, p. 8, "*quadrisulcatus*"; HNR, 1933, p. 141).

Chlaenius nigricornis

Sweden. Skå Sjörup, Södra-Vallösa, "Warm period" (G. Andersson, 1880, p. 20, HNR, 1933, p. 141).

669 *Cicindela campestris*

Denmark. Sjælland, Femsølyng-Mose, subatlantic (HNR, 1933, p. 122).

Clivina fossor

Sweden. Skå Toppeladugård, "Warm period" (HNR, 1933, p. 127).

Cychrus caraboides

Sweden. Sma Djursdala region, late-boreal (Sundelin, 1917, p. 158). Dlr Alvdalen, Lokbodarne, late-atlantic, thorax (G. Samuelsson, PU !). Ogl Järnlunden, sub-boreal (Sundelin, *l.c.*). Dlr Stora-Tuna, Skärsjö, "Warm period," elytra of 2 specimens (E. Bergquist, SG!). Skå Skurup, Saritslöv, "Warm period" (Kurck, 1917, p. 51; HNR, 1933, p. 125).

Denmark. Sjælland, Lillemose and Femsølyng-Møse, "Warm period" (HNR, l.c.).

Diachila arctica

Sweden. Ång Härnön, (Riss-Würm ?-) interglacial (LTH, 1948a, p. 8).

Diachila polita

Sweden. Ång Härnön, (Riss-Würm ?-) interglacial (LTH, 1948a, p. 8); Långsele, (Riss-Würm-) interglacial, fragment of an elytron (Sandgren, SG!).

Elaphrus cupreus

Finland. Nl Kyrkslätt, late postglacial (PPP, 1911, pp. 13, 36).

Elaphrus lapponicus

Sweden. Ång Långsele, (Riss-Würm-) interglacial (LTH, 1948a, 8).
Denmark. Jutland, Nørre-Lyngby, late-glacial (HNR, 1933, p. 126).

Harpalus nigritarsis

Sweden. Ång Långsele (Riss-Würm-) interglacial (LTH, 1948a, p. 9).

Leistus rufescens

Finland. Om Lappajärvi, Kärnä, Littorina, 1 elytron (BCM, MH!).

Loricera pilicornis

Denmark. Sjælland, Refsnæsgaard, "Warm period" (HNR, 1933, p. 126).

†*Nebria fossilis* Kolbe

Sweden. Skå Öja, late-glacial (Holst, 1908, p. 5; Kolbe, 1933, p. 212; HNR, 1933, p. 126).

Nebria gyllenhali

Sweden. Jtl Pilgrimstad (Riss-Würm-) interglacial (LTH, 1948a, p. 7).
Denmark. Sjælland, Vintappermosen, late-glacial (HNR, 1933, p. 125).

Notiophilus aquaticus

Sweden. Ång Härnön (Riss-Würm ?-); Jtl Pilgrimstad (Riss-Würm-) interglacial (LTH, 1948a, p. 7). Skå Svedala and Västra-Nöbbelöv, Mossby, late-glacial (HNR, 1933, p. 126, "*coriaceus*").

670 *Oodes helopioides*

Sweden. Skå Skurup, Munkholms-mosse, "Warm period" (Kurck, 1917, p. 55). The record mentioned from the interglacial deposits near Ång Härnön (Mjöberg, 1916, p. 7) must be erroneous (LTH, 1948a, p. 5).

Finland. Om Kärsämäki, Kintasahonräme, early atlantic, "Warmth flora," 1 elytron (BCM, MH!). Ik Sakkola, Isosuo, late postglacial (PPP, 1911, pp. 24, 36; MH!).

Denmark. Jutland, Tuesbøl, (Riss-Würm-) interglacial (HNR, 1933, p. 141).

Patrobus assimilis

Sweden. Ång Långsele, (Riss-Würm-) interglacial (LTH, 1948a, p. 9). Skå Skurup, Kyrkomossen, aspenpine-zone, 1 elytron (GL!).

Finland. Om Pelso, early atlantic, 1 elytron (BCM, MH!). Oa Lapua, early atlantic, 1 elytron (GH!). Ik Rautu, Osmina, late postglacial, 1 elytron (LBH, MH!). Om Kannus, Hietajärvi, late postglacial, 1 elytron (GH!).

Norway. Tromsö, undetermined age, 1 elytron (MT!).

Patrobus septentrionis

Sweden. Ång Långsele, (Riss-Würm-) interglacial (LTH, 1948a, p. 9). Skå Trälleborg; Svedala; Toppeladugård; late-glacial (Holst, 1908, p. 4; Kolbe, 1933; p. 210; HNR, 1933, p. 129). Jtl Ragunda, late postglacial (Sandegren, 1924, p. 45).

Denmark. Sjaelland, Jyderup and Femsølyng-Mose; Jutland, Esbjerg; late-glacial (HNR, l.c.). At least in Denmark, the subspecies *australis* may be present in part.

Pterostichus anthracinus

Denmark. Sjaelland, Femsølyng-Mose, subatlantic (HNR, 1933, p. 137).

Pterostichus ? archangelicus Popp.

Finland. Ik Kivennapa, Linnamäki, late-glacial (PPP, 1911, pp. 16, 37). This species is today distributed westward as far as the Kanin Peninsula.

Pterostichus aterrimus

Sweden. Skå Brösarp, Holmana, transition boreal-atlantic; Skurup. Sandäkra, "Warm period" (Kurck, 1917, p. 97; HNR, p. 135).

Pterostichus diligens

Sweden. Skå Åkarp region, "Alnarp River," ? preglacial (Holst, 1911, p. 40; Kolbe, 1933, p. 210). Ång Härnön, (Riss-Würm ?-), and Långsele, (Riss-Würm-) interglacial (LTH, 1948a, p. 10). Skå Toppeladugård, late-glacial (Holst, 1906, p. 8; HNR, 1933, p. 139). Dlr Älvdalen, Lokbodarne, atlantic, 2 right elytra (G. Samuelsson, PU!). Pil Arvidsjaur, Långmyren, late postglacial (v. Post, 1906, pp. 254 ff.), 1 elytron (PU!). Dlr Stora-Tuna, Skärsjö, "Warm period," 2 elytra (E. Bergquist, SG!).

Finland. Ik Sakkola, Isosuo, and Rautu, Osmina, late postglacial (PPP, 1911, pp. 18, 23, 37); both determinations uncertain (see p. 659). Tb Pihtipudas, Alvajärvi, atlantic or early sub-boreal, 1 elytron (BCM, MH!). Al Kökar, Tell-mossen, later Littorina, both elytra (BCM, MH!).

Denmark. Sjælland, Femsølyng-Mose, "Warm period" and subatlantic (HNR, 1933, p. 138).

671 *Pterostichus gracilis*

Sweden. Skå Löddesborg, "Alnarp River," ? preglacial (Holst, 1911, p. 40; Kolbe, 1933, p. 210; HNR, 1933, p. 137).

†*Pterostichus* (*Oreophilus*) *holsti* Kolbe

Sweden. Skå Nevishög, Torreberga, "Alnarp River," ? pre-glacial (Holst, 1911, p. 40; Kolbe, 1933, p. 210; HNR, 1933, p. 139).

Pterostichus minor

Sweden. Gtl Sproge, Snoder, Littorina, elytron without apex (v. Post, 1903, p. 356, "carabid,"; PU!). Ång Bjurholm, Majamyr, ? sub-boreal (v. Post, 1906, pp. 234 ff.), elytron without apex (PU!). Nbt Älvsbyn, Borgfors, probably sub-boreal, 1 elytron (G. Nordwall, MH!).

Finland. Om Lappajärvi, Kärnä, Littorina, 1 elytron. Sb Viermä, Kallolampi, probably Littorina, 2 elytra. Om Toholampi, Littorina, 1 elytron. Ob Alatornio, late postglacial, 1 elytron (all BCM, MH!).

Pterostichus niger

Sweden. Skå Skurup, boreal; Sjörup, Södra-Vallosa and Hassle-Bosarp, "Warm period" (HNR, 1933, p. 136). Gtl Fröjel and Havdhem, early postglacial (Sernander, 1894a, pp. 43, 62). Dlr Stora-Tuna, Skärsjö, "Warm period," 2 elytra (E. Bergquist, SG!); Evertsberg, sub-boreal, 1 almost complete specimen, bordering sub-boreal-subatlantic, 1 elytron (G. Samuelsson, PU!). The determination of a late glacial record from Skå Bjärsjölagård (G. Andersson, 1889, p. 10) is uncertain.

Denmark. Sjælland, 2 localities; Jutland, 3 localities; 4 from the "Warm period," 1 subatlantic (HNR, 1933, pp. 135–136).

Pterostichus nigrita

Sweden. Gtl Sproge, Snoder, boreal, elytron without apex (v. Post, PU!). Skå Toppeladugård, "Warm period" (HNR, 1933, p. 136). Dlr Stora-Tuna, Skärsjö, "Warm period," 4 thoraces, 4 elytra (E. Bergquist, SG!).

Finland. Om Sievi, Mustalampi, probably Ancylus, 1 elytron. Ob Ranua, Jänkälampi, early atlantic, 2 elytra, Om Pelso, early atlantic, 2 elytra; Haapajärvi, Pekanneva, early atlantic, 1 elytron; Vieremä, Kallolampi, Littorina, 2 elytra; Lappajärvi, Kärnä, Littorina, 3 elytra; Happajärvi, Murisjärvi, postglacial, 1 elytron; Sievi, Kukko, postglacial, 1 elytron; Rautio, Iso-oja, postglacial, 1 elytron (all BCM, MH!). Ik Rautu, Osmina, late postglacial, 1 elytron (LBH, MH!). Nl Kyrkslätt and Sb Jorois, late postglacial (PPP, 1911, pp. 13, 29, 37).

Denmark. Jutland, Maarup, (Riss-Würm-) interglacial (HNR, 1933, pp. 118, 136, 286). Sjælland, Femsølyng-Mose, "Warm period" and subatlantic, a late-glacial record from Fyen is uncertain (HNR, 1933, p. 136).

Pterostichus oblongopunctatus

Sweden. Skå Sjörup, Bräkna-Mosse, boreal (G. Andersson, 1889, p. 23); Toppeladugård, "Warm period" (HNR, 1933, p. 135). Ång. Bjurholm, Majamyr, ? sub-boreal (v. Post, 1906, pp. 234 ff.), 2 damaged elytra (PU!).

Finland. Om Vieremä, Kallolampi, Littorina, 1 elytron (BCM, MH!).

Denmark. Sjælland, Femsølyng, "Warm period" (HNR, l.c.).

†*Pterostichus primarius* Kolbe

672 *Sweden.* Skå Nevishög, Torreberga, "Alnarp River," ? pre-glacial (Holst, 1911, p. 40; Kolbe, 1933, p. 212; HNR, 1933, p. 139). Closely related to *P. aethiops* (specifically different?).

Pterostichus punctulatus

Denmark. Jutland, Kandestederne, "Warm period" (HNR, 1933, p. 134).

Pterostichus strenuus

Denmark. Sjælland, Femsølyng-Mose, "Warm period" and subatlantic (HNR, 1933, p. 138).

Pterostichus (*Lyperophorus*) *vermiculosus* Men.

Sweden. Ång Härnön, (Riss-Würm ?-) interglacial (LTH, 1948a, p. 10).

Finland. Ik Kivennapa, Linnamäki, late-glacial (PPP, 1911, pp. 16, 37).

A Siberian species, today distributed westward only as far as Pechora.

Pterostichus vernalis

Sweden. Skå Skurup, Kallsjö and Sandåkra; Önnarp, Sote-mosse, "Warm period" (HNR, 1933, p. 134).

Denmark. Sjælland, Femsølyng, subatlantic (HNR, l.c.).

Pterostichus vulgaris

Sweden. Dlr Stora-Tuna, Skärsjö, "Warm period," 1 elytron and remains of a thorax (E. Bergquist, SG!).*

Denmark. Sjælland, Femsølyng-Mose, Jutland, Skagen; "Warm period" (HNR, 1933, p. 138).

Pterostichus (*Cryobius*) sp.

Sweden. Ång Härnön, (Riss-Würm ?-) interglacial (LTH, 1948a, p. 10).

Trechus rivularis

Sweden. Dlr Älvdalen, Lokbodarne, atlantic, 1 elytron (G. Samuelsson, GU!).

Trechus secalis

Sweden. Dlr Älvdalen, Lokbodarne, atlantic, 3, elytra (G. Samuelsson, GU!).

So altogether 67 species of the present-day Fennoscandian carabid fauna, i.e. 19%, have been found in subfossil condition within the limits of the region or in Denmark; in addition there are 7 species—including 3 ostensibly extinct species—that no longer occur there. This is not an inconsiderable component, and it can be expected that these records will materially clarify the faunal history.

In summary, the following conclusions with regard to the Fennoscandian fauna can be drawn from the subfossil carabids so far available:

673 1. In the pre-glacial time in Fennoscandia—so far as the age and animal determinations are reliable**—there were some species different from those found today. Their climatic requirements cannot be ascertained. For other reasons as well we must reject the idea that the members of our recent carabid fauna in any part of Fennoscandia represent the direct and *in situ* surviving descendants of the Fennoscandian Tertiary fauna.

2. During the last (Riss-Würm-) interglacial period—the only one from which definitely datable records are available—the climate was in part distinctly temperate, even in northern Fennoscandia. The finding of two curculionids (*Ceuthorrhynchus quadridens* Panz., *Orobites cyaneus* L.) north of the limit of their recent area (Lindroth, 1948a, pp. 18, 26) suggests that the climate was at least not cooler than today. Jessen and Milthers (1928, pp. 334 ff.) have clearly shown that the climate of the last interglacial period in Denmark was in part much warmer than today. It is unlikely that this should not also apply to Fennoscandia.

*In the same peat sample 2 elytra of the silphid *Pteroloma forsströmi* Gyll. were found.

**Concerning the present concept of the "Alnarp River," see Brotzen (1948, p. 5) and Sandegren (1948, p. 39). The latter regards the deposits as interglacial.

3. During the last glaciation (Würm), at the southern edge of the northern inland ice, there was a fauna which—like the flora—included many of the characteristic members of our fjeld fauna. Also represented were species (*Amara alpina*, *Bembidion hasti*, *Elaphrus lapponicus*) today missing from the Central European mainland. Such facts could be cited to support the view that our fjeld fauna, following the ice edge, has immigrated from the south. On the other hand, there are also to be found in the same late-glacial deposits species that have not succeeded in this, such as †*Nebria fossilis*, *Bembidion* (?) *glaciale*, *B. repandum*, *Pterostichus vermiculosus*, and also *Simplocaria deubeli* Gnglb. (Henriksen, 1933, pp. 109, 174, 296), *Thanatophilus trituberculatus* Kirby (*Silpha baicalica*, l.c., pp. 165, 290), and †*Donacia extincta* Kolbe (1933, p. 213).

4. During the postglacial warm period (chiefly in the boreal and atlantic periods, around 7000–2500 B.C.) the more demanding elements of the fauna were certainly favored in the same way as those of the flora. This is evident from the wide distribution of *Trapa natans* at that time (Malmström, 1920;
674 Jessen and Milthers, 1928, Fig. 35) and of the marsh turtle, *Emys orbicularis* (Isberg, 1930) (concerning the warm period, see also the summary by Nordhagen, 1933, pp. 155 ff.). Two cases among the subfossil carabids may be cited. First, *Calosoma sycophanta*. As elucidated above (p. 621) this is presently a transgrading (i.e. nonresident) species in Fennoscandia. The three known Swedish subfossil finds are located north of the present transgression region (if the isolated recent locality in Dlr is excluded). Theoretically even the subfossil finds could be the remains of accidental immigrants. But if it is taken into account that the chance of discovering a subfossil of *Calosoma sycophanta* is much more remote than of coming across the magnificent living insect, it must be assumed that the species actually had a wider distribution in Sweden earlier in the postglacial period. And since at one locality (Dsl Mellerud) 2 subfossils were found together it is even possible that the species at that time was actually resident here (Lindroth, 1942). The most interesting fact is that as early as in Ancylus time this species occurred as far north as Upl.

The second example is provided by *Oodes helopioides*. The fossil find near Om Kärsämäki, Kintasahonräme, is though not far outside the northern limit of the present area. Found at the same place were subfossils of markedly heat-requiring plants (including *Najas flexilis*), which undoubtedly originate from the "Warm period."

The sub-boreal finds of *Pterostichus niger* near Dlr Evertsberg seem to lie outside the present area of the species as well.

Still more remarkable as testimony of the "Warm period" is the record of the heteromeran *Platydema violacea* in *Trapa*-gyttja[†] near Nl Karis (G. Andersson, 1898, p. 40; Poppius, 1911). This characteristic species—which

[†](= mud of organic material [limnological deposits] which formed during deficiency of oxygen; suppl. scient. edit.)

can hardly be wrongly identified—is missing from the present-day fauna of Finland.

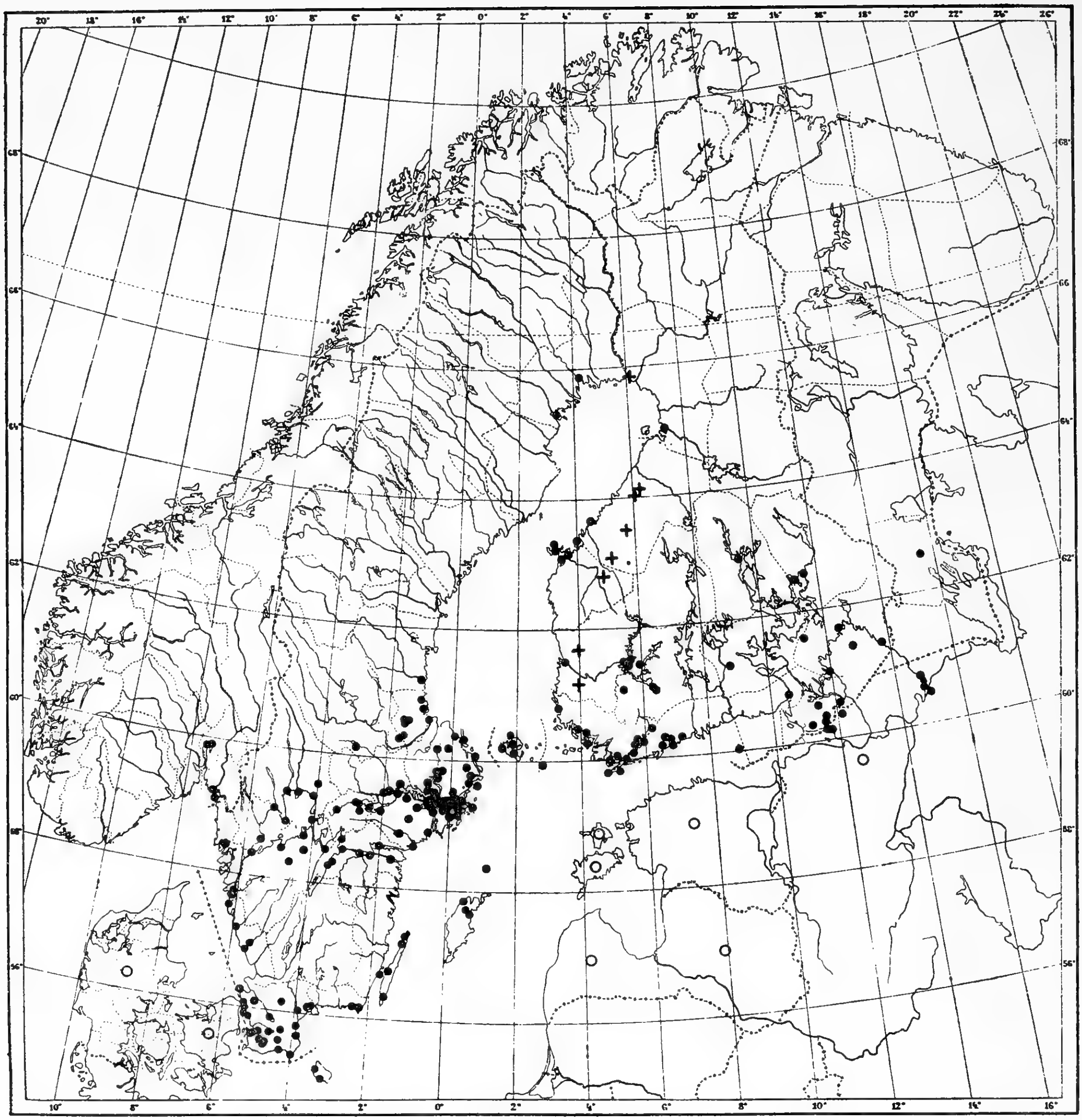
An instructive example of how the present-day area can be supplemented by fossil records is provided by *Agonum thoreyi* (Fig. 95). They fill the gaps between some of its widely separated localities east and north of the Bothnian Sea. Whether climate influenced its retreat might seem uncertain in view of the records from Lk Muonis, 32 Salten, and 41 Vaggatem. But all three records are still somewhat doubtful; no record material was available from the two Norwegian localities and from Muonio where are also other improbable
676 records (such as *Acupalpus dorsalis*, *Bembidion ustulatum*). It looks as though the occurrence of *Agonum thoreyi* at the northern end of the Gulf of Bothnia is a relict from the postglacial "Warm period" (see p. 692).

How important the fossil record of a species of animal is for the history of the animal and for our idea of the environmental conditions then depends on the constancy of the ecological valency of the species.

By "ecological valency" Hesse (1924, pp. 16–17) means: "the full scope (amplitude) of the conditions for life within which a species of animal is able to prosper." It is thus a measure of the "stenotopy" of the animal (pp. 563 ff.). The question is whether the requirements for life determined for the present-day animal (experimentally or in nature) are true for individuals and populations of the same species in past ages. If *not*, we must be very cautious in judging prehistoric climatic and other conditions from fossil records.

The zoologists principally concerned with this problem (for example, Nehring, 1890, p. 134; Warnecke, 1934, 1936a; Reinig, 1938, pp. 13 ff.) are unanimous that it is impossible to postulate the constancy of ecological valency of every species of animal. This orthodox notion would negate the whole concept of evolution. The "species" is often a heterogeneous conglomerate of several biotypes (ecotype; Turesson, 1927, etc.). As a "working hypothesis" (Warnecke, 1936a, p. 6; cf. on the contrary, Schultz, 1930, 1934a, 1934b) the "constancy rule" is very useful. If we work with *short periods* of time (such as within the limits of the Quaternary) and avoid drawing far-reaching conclusions from the fossil occurrences of a *single* species, the hypothesis gains a high degree of credibility. Nobody can doubt the arctic character of the climate—as manifested by the subfossil plants and animals—along the late-glacial ice edge in the southern Baltic region, or the wealth of paleontological evidence in favor of a postglacial Warm period (also see p. 687).

677 But one should not posit precise thermal changes especially of the *macroclimate,* on the basis of the fossil record of a solitary species of animal or plant, as has been done, for instance, by A.C. Johansen (p. 663) with reference to Molluska. Limnetic animals, and also plants (see Samuelsson, 1934, pp. 144–145), are particularly unsuitable for this purpose (Wesenberg-Lund, 1909, pp. 456 ff.), and even the distribution of terrestrial mollusks in Scandinavia shows little correspondence with the Johansen's contentions (Økland,



675 Fig. 95. *Agonum thoreyi.* Fossil (postglacial) records are marked with crosses. Three northernmost recent localities (Norway, Finland) (cf. map in Part II) are omitted as not being reliable.

1925, p. 153). Only forest trees may serve as reliable objects for this purpose, as illustrated chiefly by G. Andersson (1902b, 1910) on *Corylus*. Insects are dependent on *microclimate* (pp. 498 ff.) to such an extent that their dependence on "regional climate" is very indirect. For this reason I do not believe that Henriksen (1933, pp. 286–287) is correct in assuming that *Otiorrhynchus dubius* Ström is a species whose thermal requirements altered in the direction of "cold" during the Würm Ice Age, a view already contradicted elsewhere (Lindroth, 1935a, p. 612; Warnecke, 1936, p. 8).

However, it seems to me that we can draw the following modest conclusion on the basis of subfossil records of insects: A Quaternary period during which *more than one* species of insect is found to have occurred north or south of its present area may be presumed to have been warmer (or colder) than the climate there today.

Relicts

In none of the distribution phenomena is the dependence of the present-day area of an animal or plant species on historical factors and on the conditions of distant part so evident as in the case of relicts. These are "living fossils."

Researchers have greatly differed on the true or appropriate meaning of the term "relict." This is not the place to discuss the whole history, but it is hardly possible to define my own principal concept without discussing earlier views.

The term seems to have been used in print for the first time by Peschel (1875, p. 207; "Relictenfauna"). In Nordic literature the expression was introduced by botanists, especially by Sernander (1894b) and Nathorst (1895). The best botanical definition of the term may be Th.C.E. Fries' (1913, p. 392:
678 ". . .that by this is meant the occurrence of a plant or plant community at a location where the plant or plant community does not occur today, so long as there are no prehistoric, now nonoperative factors in the history of immigration to account for it." Zoological definitions agreeing in content have been provided by Ekman (1915) and v. Hofsten (1911, pp. 59–60; 1913; p. 34). A particularly clear definition is given by the first of these authors (Ekman, 1915, p. 5; and 1922, p. 278, in Swedish): "A species is a relict in a region where its existence [1935, p. 201, altered to 'presence'] proves that the species itself or its primitive form was left there under natural conditions now alien to the region in question." The slightly altered wording of the definition in his contribution of 1935 (p. 201) adds that a relict species should occur "isolated from its main area of distribution." As also emphasized by v. Hofsten (1911, p. 59), the relict concept must be defined both *temporally* and *locally*.

Even if we ignore the very broad idea of the term "relict," such as that given by Wesenbeg-Lund (for example, 1910, pp. 29 ff.)—which must be rejected (see, for instance, A.C. Johansen, 1908)—it still admits of varying limits. Ekman holds that only those populations of species deserve to be called "relict" which, since becoming relict, have continued to live *in situ* until present-day, whereas all populations that have emigrated from a former relict center should be called pseudorelicts (Nathorst, 1895; or secundorelicts). In botany this differentiation of terminology is used still oftener, especially by Stoller (1921, p. 420): "From the paleobotanical viewpoint the relict character of a plant for a particular locality can be recognized only if evidence can be produced that the species has lived at this location isolated from its present-day closed district of distribution since its immigration, which took place during an earlier period."

In limnetic organisms it is often possible to provide proof—or evidence supporting high probability—that the species concerned must have lived an uninterrupted life in this or that lake since the original isolation. This is not possible in the case of terrestrial flora; the assumption of this requirement by Stoller signifies "as good as complete elimination of the relict concept from the science of phytogeography" (Wangerin, 1924, p. 61). It is still worse in the case of the mobile elements of the terrestrial fauna (Lindroth, 1943a, p. 140).
679 The following is an attempt to arrive at a consistent division of the relicts (s.l.) among terrestrial organisms into "pseudorelicts" and "true relicts":

a. "Pseudorelicts," which could not have lived *in situ* continuously. Examples: *Alchemilla alpina* and *Rhodiola rosea* in western Sweden, where they grow largely below the shoreline of the Littorina period (Sernander, 1894b; Nathorst, 1895; Lid and Zachau, 1929); *Oodes gracilis* in the Stockholm region where the inhabited lakes (with two exceptions) were first formed in the subatlantic period (Lindroth, 1943a).

b. All remaining "relicts" (*s.l.*), of which it cannot be stated whether they are true relicts (in Stoller's and Ekman's sense) or pseudorelicts. I cannot imagine what kind of evidence could prove the uninterrupted occurrence of a terrestrial plant or a terrestrial animal within a narrowly delimited terrain extending, say, over a few square kms.

Hence for practical reasons I accept Drude's (1918, pp. 44–45) and Wangerin's view (1924, p. 67) in phytogeography. The latter (l.c.) writes: "secondary displacements of locality . . . even under the conditions of a definite, locally restricted new dispersal from old places of subsistence . . . in no way detract from the relict nature so long as a new immigration from outside does not take place, or the new dispersal does not assume the level of an extensive expansion, a case which probably has yet to be realized." The term "pseudorelict" should not be rejected, but it must be subordinate to the broad term "relict," not on a level with it. The above definition by Ekman also fits this broadened idea of a relict, provided his expression "region" is geographically not inter-

680 **Table 37. The most isolated localities or more or less close locality-groups of carabids in Fennoscandia. Only cases where the gap is situated within the region (including eastern Baltics and Denmark) are included. Records in the Russian part (before 1939) and on islands are excluded**

Species	Isolate	Nearest locality	Distance in km	Assumed cause of isolation
1	2	3	4	5
Bembidion aeneum	Ks Paanajärvi	31 Bodö	706	Relict
Agonum mannerheimi	12 Vardal	St Yläne	655	Relict
Harpalus rubripes	31 Bodö	24 Vågå	655	Import ?
Agonum longiventure	Upl, Dlr, Gst, 5 localities	Estonia, Narva	617	Relict
Dromius longiceps	Ob Hailuoto	Ab Åbo	529	Relict ?
Dyschirius helléni	24 Vågå	Lyl Tärna	517	Relict, also insufficiently explored
Chlaenius costulatus	Ok Ruthinassalmi	La Lampis (Lammi)	504	Migration
Trechus fulvus	26 Hitra	6 Nedstrand	504	Relict, also insufficiently explored
Agonum ruficorne	26 Vallersund	7 Bergen region	441	Import ?
Bembidion minimum	26, 28, 2 localities	2 Oslo	441	Relict
Tachys bisulcatus	Lyl Sorsele	Hls Los	440	Insufficiently explored
Amara convexiuscula	Ik Kuokkala	Ab Åbo	428	Import ?
A. nigricornis	21 Sirdal	24 Skogseter	403	Relict
Dromius quadrinotatus	26 Hitra	18 Tyssedal	403	Import ?
Dyschirius obscurus	Li Ivalo	Ob Uleåborg	403	Migration ?
Pristonychus terricola	27 Trondheim	2 Oslo	403	Import ?
Pterostichus niger	35, 36, 2 localities	32 Hammernes	403	Relict ?
Chlaenius nigricornis	Nbt Neder-Kalix	Sb Kuopio	397	Relict ?
Trechus micros	27, 2 localities	2 Oslo	384	Relict
Pterostichus vulgaris	Lk Pelkosenniemi	Om Haapavesi	365	Import
Bembidion transparens	33, 35, 3 localities	Li Enare	353	Relict
Agonum mülleri	Ks Kuusamo	Kb Polvijärvi	347	Import ?
Bembidion grapei	6, 27, 2 localities	24 Vågå	346	Relict
Amara lucida	South Finland 2 localities	North Kurland	340	Migration ?
Cicindela campestris	35 Tromsdal	31 Bodö	340	Relict ?

Species	Isolate	Nearest	Distance in km	Assumed cause of isolation
Bembidion nigricorne	Hls Los	Nke Laxå	328	Relict
Calosoma reticulatum	Boh Fors	Skå Trolle-Ljungby	328	Relict ?
Dyschirius angustatus	Vrm Höje	24 Vågå	328	Relict ?
Bembidion hyperboraeorum	Ok Sotkamo	Ks Sallo	315	Migration ?
Trechus discus	27, 2 localities	Hls Los	309	Relict ?
Bembidion siebkei	Ks Paanajärvi	Li Kyrö	302	Relict
Calosoma sycophanta	Dlr Korsnäs	Vgl Fårdala	302	Migration ?
Dromius quadrimaculatus	Ång Docksta	Upl Älvkarleby	302	Migration
Trachypachys zetterstedti	Southwestern Finland, 3 localities	Estonia, Narva	302	Dying out species
Amara curta	28 Tynes, Verdal	20 Geiranger	290	Relict ?
A. erratica	Ik Metsäpirtti	Kn Juustjärvi	283	Relict
Dromius fenestratus	Ok Sotkamo	Kl Parikkala	283	Insufficiently explored
Brachynus crepitans	Nl Hangö	Stockholm	278	Migration
Dyschirius politus	Ks Salla	Ob Uleåborg	277	Relict ?
Pterostichus adstrictus	Små, 2 localities	Vrm Forshaga	277	Relict
Dyschirius angustatus	Ks Paanajärvi	Lp Lutto	265	Relict ?
Abax ater	Southeastern Norway, 2 localities	Jutland	252	Relict
Agonum gracilipes	Norway, Sweden, Finland (several localities)	–	>250	Migration

Agonum bogemanni, with several highly isolated, old, mostly poorly determined localities may be added. This species is certainly dying out in our region.

preted too narrowly. If one wishes to emphasize an established uninterrupted life *in situ* the word "eurelict" can be used.

On the other hand, on two other counts I wish to modify Ekman's definition. First, it is not clear why relicts could not be separated under systematic entities other than "species." Second, the latter qualification "isolated from the main region of distribution" (Ekman, 1935, p. 201) does not seem to be necessary, especially since it is not always possible to ascertain the "main region of distribution." For instance, we may study the total distribution of *Pteros-*

tichus kokeili Mill. which is split into small isolates (Holdhaus and Lindroth, 1939, Plate VIII); even in the copepod *Limnocalanus grimaldii* (Ekman, 1922,
681 pp. 278–279; 1935, pp. 203–204) a main area is not readily evident. Although this animal in the Baltic Sea basin and in the neighboring lakes was earlier considered as a separate species (*L. macrurus*), Ekman (1922) pronounced this a relict as a whole, and in principle there is nothing against this view. One should also be able to use the word "relict" for the remnants of a species of animal or plant that is dying out, such as *Hatteria* (*Sphenodon*) even if perhaps internal causes have been more responsible than external.

In light of these objections the following definition of the term "relict" seems to fill the bill: A relict is a stock of a genetic-taxonomic unit (subspecies, species, genus, etc.) that is functionally separated from the remaining (as a rule wider, possibly prehistoric) area of the unit and was not able to invade the isolate during present natural conditions.

The actual problem—not just one of terminology—is to draw the distinction between relicts and immigrants (autoimmigrants—Ekman), between remnants and advance posts. For this purpose we will now take the carabid material as the basis.

The prime characteristic of relicts is their isolated condition. Obviously we must draw up a list of the especially isolated localities or locality-groups of carabids in Fennoscandia in order to assess their possible relict character. Table 37 gives such a list. It omits all insular records, which have been sufficiently dealt with in a separate section (pp. 198 ff.), and localities whose nearest occurrence lies outside the limits of Fennoscandia. But to the extent that they are to be considered as relicts, these cases are included in the summary below.

Speculative causal explanations for the isolates are suggested by the table itself. A survey shows:

The definite isolates in 43 Fennoscandian carabids are divisible as follows:

	a. Relicts	17 species	— 25 species
	b. Possible relicts	8 species	
	c. Accidental migrants	4 species	— 8 species
	d. Probably accidental migrants	4 species	
682	e. Displaced by civilization	3 species	— 8 species
	f. Probably displaced by civilization	5 species	
	g. Insufficiently explored	2 species	— 2 species.

There remain a considerable number of carabid records in Fennoscandia that may be considered relicts with fairly high probability but are not isolated so far from the "main area" as to be included in Table 37. In the succeeding causally arranged list of relicts such cases are included if they are clear enough, along with species whose Fennoscandian area as a whole is relict-like.

In accordance with the definition, all relicts go back to a time when natural conditions differed from today's. Depending on the decisive environmental factor, at that time more favorable for the species in question, an appropriate

prefix precedes the word "relict". We speak of "heat relicts," "marine relicts," etc. The possible relicts among the Fennoscandian carabids seem to belong to one of the following four categories (illustrated here by especially good examples):*

A. Cold Relicts

Geological and paleontological records show that during the first part of the late-glacial period definitely cold-requiring (arctic [see alpine] and subarctic [see subalpine]) flora and fauna lived at the southern edge of the Würm Ice in northern Central Europe, and in the parts that were the first to become ice-free—at least in Denmark, Skåne, and the Isthmus of Karelia. It is thus quite conceivable that even in the more southerly parts of Fennoscandia pronounced Nordic plants and animals survived at microclimatically favorable places as relicts from this distant past. In the later postglacial period the Subatlanticum† signified a climatic deterioration (including a decline in temperature), from which relicts can also be expected south of today's continuous area.

The presumed cold relicts are arranged here geographically for the sake of simplicity.

683 a. In south-central Sweden.

Nebria gyllenhali — *Pterostichus adstrictus*

The following predominantly Nordic species are more frequent and abundant in the southern Swedish highland or its margins:

Cymindis vaporariorum — *Patrobus assimilis*
Miscodera arctica — *Trichocellus cognatus.*

Only the localities of *Pterostichus adstrictus* and of two other Coleoptera, *Otiorrhynchus dubius* Ström (maps in Henriksen, 1933, p. 294; Holdhaus and Lindroth, 1939, Plate XVII), and in particular *Evodinus interrogationis* L. (Fig. 96) are markedly isolated. A counterpart in the flora is *Saussurea alpina* (Erlandsson, 1940). Actually the south Swedish highland has climatically such a Nordic imprint (pp. 463, 474) that even much more cold-requiring forms might have been expected there.

b. Along the coast of Bohuslän.

Bembidion virens

The counterparts in the flora are *Alchemilla alpina* and *Rhodiola rosea* (Lid and Zachau, 1929).

*Good examples of relicts attributable to periods of drier or more humid climate are scarcely met with among our carabids (however, see *Calosoma reticulatum* and *Abax ater* under "heat relicts").

†(cf. Table 36, p. 661; suppl. scient. edit.).

c. On Gotland.

Miscodera arctica
Nebria gyllenhali
Patrobus assimilis

Only in *Nebria* is the isolation of course much greater than that due to the location of the island itself, but the two others have a markedly Nordic character as well (concerning *Miscodera*, see Fig. 56, p. 424).

The best counterparts in the flora are *Bartschia alpina* and *Pinguicula alpina*.

d. In southern and central Finland.

Amara erratica
Elaphrus lapponicus
Patrobus septentrionis (s. str.)
Pelophila borealis.

Possibly also *Bembidion grapei* and *Trichocellus cognatus.*

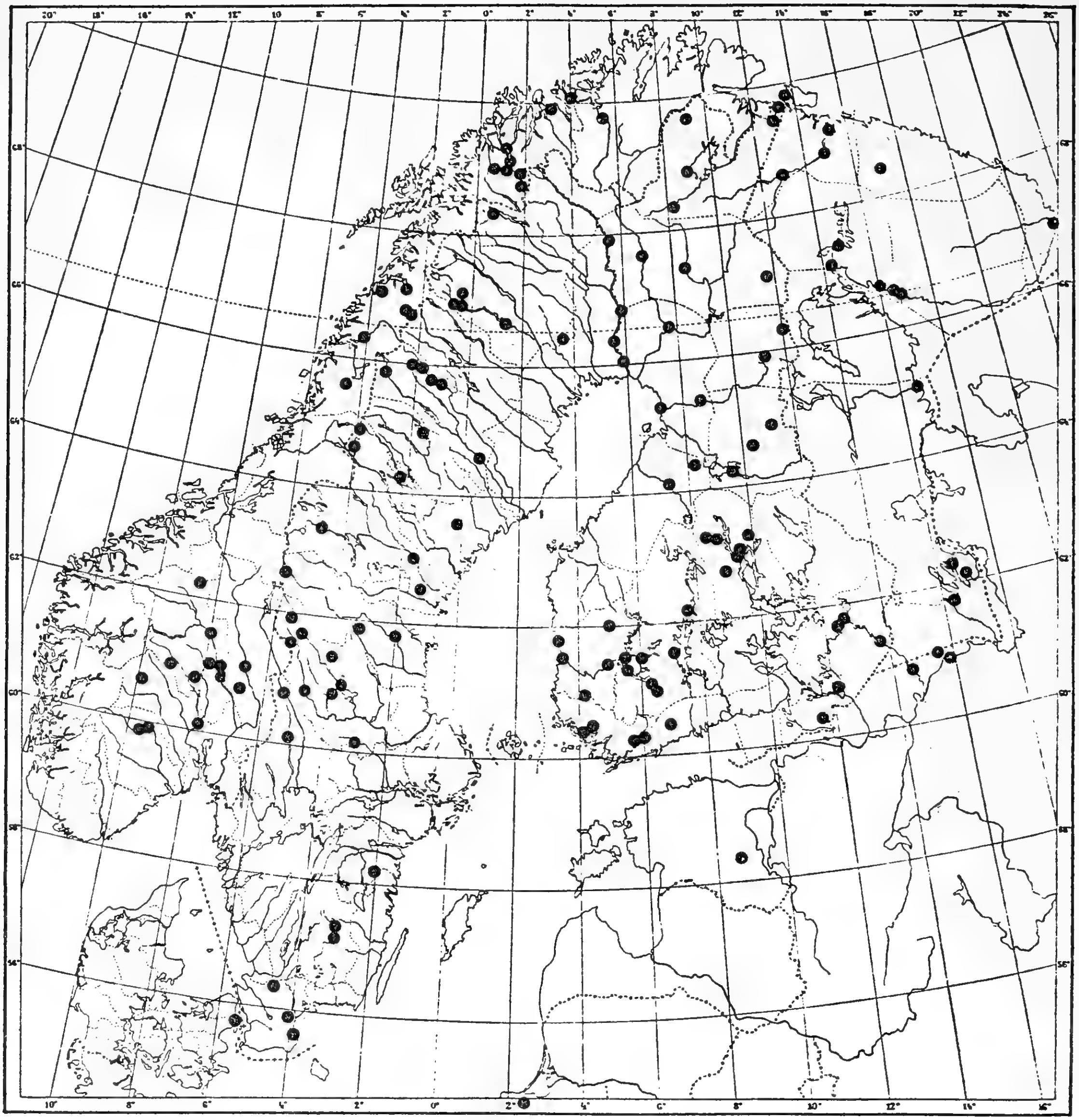
Elaphrus and *Pelophila* have also been found at one locality each in the eastern Baltic region. A far more isolated relict occurrence in southern Fennoscandia is shown by *Simplocaria metallica* Sturm (Fig. 106, p. 739).

Further information on the isolated record of 1 specimen of *Patrobus septentrionis* near Kb Juuka, July 5, 1941, is provided by Krogerus (in litt.). The
685 insect was found near Koljunkorpi close to the highest point of Juuanvaara at a height of about 300 m (i.e. a supra-aquatic region) on a steep north-facing slope on the bank of a brook emerging from a spring. The bank was stony with *Sphagnum* between the stones (*S. riparium*, *S. girgensohnii*, *S. apiculatum*). *Nebria gyllenhali* was found at the same place.

In all the species included under a–d above, the isolation, which could indicate relict character, is not clear. At best it is seen in *Pterostichus adstrictus* in Små and *Nebria gyllenhali* in Gtl. In the former species the nearest localities along the lower reaches of the River Klarälven in Vrm, are probably the result of a water transport by the river (Palm and Lindroth, 1936, p. 40). *Cymindis vaporariorum* and *Patrobus assimilis*, which lack any distinct "zone of obliteration," are functionally brachypterous and therefore colonize new habitable regions relatively slowly.

The thermophobic characters of the presumed cold relicts is clear in some cases. In the southern sub-areas they are frequently inclined toward stenotopy (cf. p. 567), sometimes on the edge of cold water (rivulets, deep lakes, the sea): *Bembidion virens*, *Nebria gyllenhali* (Holdhaus and Lindroth, 1939, p. 268), *Patrobus septentrionis* and sometimes in bogs; *Patrobus assimilis*, *Trichocellus cognatus*.

In the case of flying species it is not possible to prove that they did not colonize their southernmost, more or less relict-like isolated localities by accidental migration in recent time. But certain facts discredit that: the marked Scandinavian southern limit of *Amara erratica* and the distinct northern limit of the southern Finnish stock of *Nebria gyllenhali*; the clear bicentricity of



684

Fig. 96. *Evodinus interrogationis* L.

Northwest European distribution. Compiled from literature and larger collections (summarized in Holdhaus and Lindroth, 1939, p. 199). This map is less complete than the maps of Carabidae but clearly shows the relict occurrence in southern Sweden.

Elaphrus lapponicus in the fjeld regions; the not yet resolved bicentricity of *Cymindis vaporariorum*, *Miscodera*, and *Trichocellus cognatus*, which is maintained by a narrow but certainly real gap in Jtl. All these limits are dynamically (dispersal-biologically) determined and therefore show that the species concerned at present lacks any pronounced capability of dispersal.

Naturally there always occur small displacements of the southern limiting localities, of the "cold-requiring species" treated here (strictly speaking they are at the most "pseudorelicts"). But the first colonization of this region by any of the species in question as far as I can judge, cannot have been recent (under present-day climatic conditions). Either they are remnants of the
686 first immigration from the south, or are evidence of numerous cold-requiring species having enlarged their area southward during a late postglacial period, i.e. during the Subatlanticum.

Sernander (1894b) considers some isolated occurrences of Nordic plants in Upl (for example, *Sceptrum carolinum* as subatlantic relicts. Wahlgren (1909; 1935–41, p. 55) similarly interprets the southern Swedish localities of Lepidoptera such as *Oeneis jutta* Hb. and *Argynnis freija* Thunb. Henriksen (1933, p. 326) believes that the clumsy flightless curculionid *Barynotus squamosus* Germ. may have immigrated to Jutland (from the north) since the postglacial warm period, where it represents a subatlantic relict. I have already contested this (Holdhaus and Lindroth, 1939, p. 258; also Spärck, 1940, p. 58). On the other hand I have applied (l.c., pp. 268–269) the same interpretation to the occurrence of *Nebria gyllenhali* at the shores of lakes Vättern and Vänern. I considered it improbable that these cold-requiring species could have survived the warm period at such advanced localities.

My opinion has changed somewhat in recent years since I have come across the manifestations of micro-climate. A macroclimatic rise in temperature, to the extent assumed for the postglacial warm period in Sweden (up to about 2°C in summer), need not necessarily have brought about parallel microclimatic changes in all biotopes. At least those places directly affected by spring water or the sea may have been thermally altered. It is perhaps no accident that of the 11 "cold relicts" mentioned above, no fewer than 7 (*Patrobus assimilis* and *Trichocellus cognatus* only in the south) are hygrophilous. It seems possible that *Nebria gyllenhali* was able to survive the warm period not only near the spring water dripping from the coastal limestone rocks of Gtl but also in the splash zone of the shores of Vättern and Vänern lakes. On Gotland the history of the flightless *Tropiphorus obtusus* Bonsd. seems to have been the same (Lindroth, 1933, pp. 347–348).

We can assume that most of the 11 presumed "cold relicts" have persisted in southern Sweden and southern Finland since the first immigration—chiefly during the subarctic period—even in today's southernmost Fennoscandian habitats. Three of these species (*Elaphrus lapponicus*, *Nebria gyllenhali*, *Patrobus septentrionis*) are known from the late-glacial deposits in Denmark

687 and/or Skåne and are therefore members—at least west of the Baltic Sea—of the original southern immigration group.

B. Heat Relicts

The assumption that these may occur in Fennoscandia is based on the view that after the last glaciation there was a period with a more favorable climate than at present, an idea which is based on such abundant and unambiguous observation material that it might be considered a fact (p. 673, and Table 36, p. 661). With the beginning of the Subatlanticum (about 500 B.C.) or shortly before that the plants and animals most susceptible to cold would have been compelled to retreat from the northern or high-altitude limits of their areas. Isolated populations would have been left behind in lococlimatically or microclimatically thermally favored places outside their continuous area.

As in the case of "cold relicts," it is most practical to divide the species in question into geographical groups. Species whose assumed relict area is strikingly isolated are marked with an asterisk (*).

a. In Tröndelag (Province 27)

**Trechus discus*	**Trechus micros*

b. Head of the Sogn (Province 19). Cf. p. 454

? Carabus cancellatus	*Harpalus tardus*
Harpalus rubripes	*Metabletus truncatellus*

c. In southeastern Norway, chiefly around the Oslofjord

**Abax ater*	*Cicindela hybrida*
?Amara montivaga	*? Lebia cyanocephala*
? Bembidion stephensi	*Licinus depressus*

d. Along the Swedish west coast

? Calosoma reticulatum	**Dromius angustus*

e. In southeastern Sweden

**Calosoma reticulatum*	*Harpalus azureus*
Carabus intricatus	

and other "limestone species" (see pp. 112 ff., 289 ff.).

f. In the central Swedish lake region. h—hygrophilous; x—xerophilous

Agonum dorsale x	**Demetrias imperialis* h
**A. lugens* h	*? D. monostigma* h
**Badister sodalis* h	**Harpalus anxius* x
**B. unipustulatus* h	**H. rufitarsis* x
**Brachynus crepitans* x	**Leistus rufomarginatus*

Licinus depressus x
? _Microlestes maurus_ x
M. minutulus x
Odacantha melanura h
*_Oodes gracilis_ h
Panagaeus bipustulatus x.

g. In lower Norrland

Agonum obscurum
? _Carabus arvensis_

h. At the northern end of the Gulf of Bothnia

Agonum thoreyi
? _Chlaenius nigricornis_
*_Dromius longiceps_
Panagaeus crux-major
Pterostichus vernalis (brachypterous form; Fig. 36, p. 378)
? _Trechus rivularis._

i. In the large northern Fennoscandian wooded region some markedly southern species become very rare and occur only at especially suitable places, which probably correspond with the well-known "southern hills" and "southern peaks" of the botanists (Andersson and Birger, 1912, pp. 52 ff.). A determination of the isolation of these populations, as well as their actual relict character, must be left for a future more detailed inventory of these places. Attention should be directed to _Harpalus latus_, _Notiophilus biguttatus_, _Pterostichus oblongopunctatus._

It is of course impossible to "prove" that these advanced more or less isolated northern occurrences of southern species are in fact relicts. For this reason only certain especially clear cases will be analyzed here.

The special situation of the inner Sogn with respect to climate was considered earlier (p. 454) and the species occurring isolated in this area were listed. Naturally they are able to live in the comparatively favorable present-day climate there. Of prime interest here is _Metabletus truncatellus_, because in Sogn it has been found exclusively in the brachypterous form (p. 454, footnote). In the present time it has not once been observed in the _Regio betulina_ (p. 446), and it is unclear how it could have reached Sogn under the prevailing conditions of the plant regions of the surrounding fjelds. Nordhagen's investigations (1933, pp. 207 ff.) in Sikkilsdal in the Jotunheimen showed, however, that in
689 these regions the timber-line was much higher in the _postglacial warm period_ probably chiefly during the Atlanticum. He concludes that in this period the fjeld passes formed an open route from the eastern valleys to the inner Sogn, even for cold-susceptible plants. _Metabletus_ may also have arrived there in this way. In the case of the likewise flightless _Carabus cancellatus_ the situation is less clear, unless it is found to be actually native to Sogn; so far only 1 specimen is available. The cited elevation of the timber-line in south-central Norway also enhanced the role of the passes leading from the Glomma and Trysil valleys into Tröndelag (Province 27), which are still wooded, as faunistic and floristic migration routes. This may well explain the noticeable isolate of

the two ecologically sister species, *Trechus discus* and *T. micros* (p. 553) in the Trondheim region.

Southeastern Norway is climatically highly favored, especially in summer (Fig. 63, p. 452), and has a correspondingly rich fauna (p. 454). Some species occur there more or less isolated, most clearly *Abax ater* and *Bembidion stephensi*. However, it is very uncertain whether the occurrence of the latter species has a relict character. The first finds, not only in the Oslo region but also near Göteborg and in southeastern Finland, were made at a later date (in the first two cases in the same year, 1929). It is therefore possible, even considering the concealed mode of life of the insect, that a late immigration is involved here. The situation is different in *Abax ater*, which is constantly flightless and has been found at two widely separated localities. Both are near the most extensive beech forest region of Norway (Hjelmqvist, 1940, p. 7), which is certainly no coincidence. The total distribution of *Abax ater* (Borchert, 1938, Plate 40) largely corresponds with that of *Fagus sylvatica* forma *typica* (Hjelmqvist, 1940, Fig. 9). In Sweden it seems to live only in beech forest (unfortunately there are no ecological data from Norway). It is well known that *Fagus* earlier had a wider distribution in Scandinavia (Lindqvist, 1931, pp. 427 ff.), and the isolated southernmost stands, if spontaneous, are to be considered as relicts. It is natural to suppose that *Abax ater* immigrated simultaneously with beech in a more humid period, and that the Norwegian occurrences are relicts. In Denmark (Sjælland) the subfossil *Abax* was found in the "beech zone" (Henriksen, 1933, p. 140). At its completely
690 isolated locality in Vgl, *Leistus rufomarginatus* may have had a similar history; of course this species is winged. But it is strange that according to Horion (1938, pp. 129, 137; 1941, p. 70) this species represents a late immigration in central and western Germany.

Among the remaining possible relicts of the "Oslo region," *Licinus depressus* is of special interest, partly because it is constantly brachypterous and partly because it shows a similar isolate in east-central Sweden. Its relict character is fairly evident. However, I am perplexed about the interpretation of *Amara montivaga*, whose remarkable expansion in Scandinavia in recent decades was discussed earlier (p. 632). The possibility cannot be ruled out that the original nucleus of this expansion was a relict population in southeastern Norway, and that climatic improvement was responsible for the new area expansion (pp. 641 ff.).

Dromius angustus is certainly a relict, not only on the Swedish west coast near Hll Särö, but generally at the Scandinavian record localities (perhaps with the exception of the newly discovered locality near Skå Hälsingborg). It is striking that, with the exception of Bornholm, this species is completely missing from Denmark, so that the Scandinavian stock has no direct connection with the south. The reason for the choice of the Särö Peninsula in western Sweden as a refuge is probably not mainly the climate. Only this place had

a continuous stand of primitive coniferous forest in the immediate vicinity of the sea (see maps in Malström, 1939). *Dromius angustus* in northern Europe is namely associated with pine forest on sand or gravel close to the sea. Otherwise the species has generally a predominantly western distribution as well. It is to be assumed that it immigrated to Scandinavia during the atlantic period, during which Gotska Sandön was formed (p. 280).

The question whether *Calosoma reticulatum* in western Sweden occurs as a relict (or generally as a resident member of the fauna) was discussed earlier (p. 455). The record on Skå is certainly of an accidental nature. Even more distinctly isolated is the area of Öland, where the species lives as a true inhabitant of the open Alvar.* It is therefore a pronounced xerophile, a relict from a warm and at the same time dry period. It might not be too bold to assign its immigration period to the Boreal, when the division of land and water in the southern Baltic Sea region was most favorable. Probably the main part of the "warm element" arrived at this time from Öld and Gtl (p. 309).

691 The most pronounced summerlike warm center in all Fennoscandia is the central Swedish lake region (Fig. 63, p. 452). There is no region quite like it, with so many undoubtedly heat-requiring species occurring isolated (p. 455). Let us inquire how far the immigration routes to this region are still open, and whether, and for which species, they were in an earlier era, i.e. let us identify the unambiguous relicts in the fauna of the central Swedish warm region.

The isolation of populations there is very different in different species. "It is easy to imagine a series of distribution maps, beginning with *Oodes helopioides*, which shows a gap already in the south across Småland, continuing through *Odacantha melanura* where this gap has grown, and direct contact westward across Lake Vänern has been lost. At the next step, represented by *Agonum lugens*, south of the central Swedish region there remain only sparse occurrences, on Öland–Gotland and Skåne; and in the case of *Reichenbachia impressa* Panz., *Psammoecus bipunctatus* Fbr., *Silis ruficollis* Fbr., *Oedemera croceicollis* Gyll., and many others exclusively on Skåne or Blekinge, the two southernmost provinces of Sweden. The next step brings us to *Oodes gracilis* and *Demetrias imperialis*. Somewhere in between is *Stenus solutus* Er., whose occurrence in Skåne is still uncertain. Nor has the little *Euconnus rutilipennis* been found so far in southern Sweden.

"This series of distribution maps places an odd appearing type like *Oodes gracilis* and *Demetrias imperialis* in its organic context at a glance. They are only the most pronounced representatives of the general trend of our thermophilous fauna, the retreat after the postglacial warm period. And this answers those who, whenever they come across a zoogeographically strange find, say it must have been introduced by man. In the case of *Oodes gracilis* the

*(Plant community consisting typically of mosses and calciphilous herbaceous plants that grow on steppelike shallow alkaline soils overlying Scandinavian limestones; suppl. scient. edit.).

question may be asked: Where from? And: Why *Demetrias imperialis* as well?" (Lindroth, 1943a, pp. 139–140).

The examples selected above are all pronounced hygrophiles, which live on the shores of eutrophic bodies of water. Undoubtedly just these biotopes around the shallow lakes of central Sweden, which are well warmed at midsummer, are lococlimatically and microclimatically favored. However, the list
692 ("f") above contains as many, more or less definite xerophiles, from which it is evident that in this part of Sweden other biotopes are favored, i.e. that the lococlimate and microclimate are everywhere thermally "tainted" by the macroclimate, as is evident from the map in Fig. 63.

Some of these xerophiles were considered earlier (pp. 113 ff.) as presumed "limestone species." Unambiguous relicts are undoubtedly *Harpalus anxius* and *H. rufitarsis*. But also the other, less isolated areas, own a more or less distinct "zone of extinction" south of central Sweden, which probably at present function as effective barriers against dispersal. Only *Microlestes maurus* (Vgl Kinnekulle) arouses doubt, since only one single macropterous specimen was found. It might not be too bold to consider all the species in list "f" as relicts. Two of these species, a hygrophile (*Badister sodalis*) and a xerophile (*Licinus*), are consistently brachypterous and are therefore hardly capable of dispersal by fits and starts.

Among species with their northern limit situated farther north, e.g. in lower Norrland, it is far more difficult to establish possible relicts, chiefly because these regions have not been so thoroughly explored that one can trust the gaps shown on the map. However, in one case, *Agonum obscurum*, this appears to be justified. This species has an unusually well-defined northern limit in Scandinavia, which in Sweden and southeastern Norway corresponds fairly exactly with the isotherms of the "critical months" (Lindroth, 1939a, p. 243), and should be climatically (thermally) determined. The record of several specimens in southern Hls near Skog, Södra-Branningen is quite isolated. The gap to the south is undoubtedly real, since this covers the region thoroughly explored by Palm (1942) on the lower reaches of the Dalälven River. From the entomologist's point of view there are many suitable biotopes for *Agonum obscurum* in the boggy forests. With respect to the development of hind wings, the species is dimorphic, but near Hls Skog only brachypterous individuals were found.

The places around the northern end of the Gulf of Bothnia, in both Sweden and Finland, apparently comprises a definite relict region. These are thermally very favored in summer (p. 461; Fig. 63, p. 452). The occurrence here of the species listed above (under "h") is in some cases very isolated, especially of *Dromius longiceps*. Even in a species like *Agonum thoreyi*, where the gap
693 on the Finnish side seems insignificant, the subfossil records (Fig. 95, p. 675) show that earlier it enjoyed much wider distribution and was much more frequent. In Vbt and Nbt I methodically searched for just this species and was

able to confirm its rarity. The only locality where it occurred in large numbers, Nbt Råneå, apparently was strongly favored thermally, since several other pronounced southern species also live here (Lindroth and Palm, 1934, p. 17). Of the 7 species enumerated above, doubtful relicts in the region considered here are *Chlaenius nigricornis* and *Trechus rivularis*, the former on account of the pronounced general tendency of the *Chlaenius* species to migrate, the latter because it is a strictly stenotopic animal which easily escapes the attention of the collector.

Moreover, in Finland there are no clear examples of heat relicts among the carabids. It is of course possible that *Bembidion nigricorne* and *B. ruficolle*, perhaps also *Amara infima* and *Tachys bistriatus*, are such. But the two latter species have a concealed mode of life and may have been overlooked. Throughout the Fennoscandian area the species of *Bembidion* are perhaps to be considered as relicts from a warmer period. In the case of *B. nigricorne* this is evident from the map on dimorphism (Fig. 44, p. 390). That *B. ruficolle* does not occur even in Sweden because of a late, more or less accidental westward advancement (as in western Germany; Horion, 1936; 1937, p. 11; 1941, pp. 123–124) is evident from the fact that the species, found before 1827, was recently rediscovered at its first record locality.

The carabids cannot help us answer the question whether in southwestern Finland, especially at the Cape of Hangö, there is a relict region for xerothermal species. Krogerus (1932, p. 250) mentions some species of insects (but no Coleoptera) for which he assumes this, among them *Sphingonotus coerulans*, which even in Sweden is regarded as a heat relict (p. 455). Palmén (1944, p. 221) is undoubtedly correct when he argues that such isolated records in the Hangö Peninsula may represent the result of late anemohydrochorous transport from Estonia. But I think he dismisses the relict problem somewhat superficially. A closer study of the flightless curculionid *Scleropterus serratus* Germ., which occurs isolated in southwestern Finland, would be very interesting in this connection. Har. Lindberg's view (1942, 1943) that *Amara crenata,*
694 *A. majuscula*, and the curculionid *Gronops inaequalis* Boh. in the Skärgård of southwestern Finland are to be considered as Ancylus relicts ("pseudorelicts") is certainly wrong (see p. 622).

Probably, the time of immigration of any of the "heat relicts" considered here cannot be established more precisely. However, on the basis of the Finnish subfossil records the maximal distribution of *Agonum thoreyi* (p. 674) might fall in the sub-boreal, and the recent finds along the Gulf of Bothnia may be considered as relicts from this period. The markedly *xerothermal* relicts (*Calosoma reticulatum*, many species of *Harpalus*, and others), which are so characteristic of Öland–Gotland, had probably already immigrated in the Boreal. During that period (Ancylus epoch) the distribution of land and water in the southern Baltic Sea region was especially favorable and some of the species concerned were flightless (pp. 298 ff.). However, among carabids there

are no such clear examples of xerothermal relicts as *Sicista subtilis* in central Scandinavia (according to Ekman, 1922, pp. 206 ff., probably a boreal relict) or *Stipa pennata* in Vgl. (according to Sernander, 1908, a sub-boreal relict).

C. Coastal Relicts

In Fennoscandia the shorelines were postglacially subjected to continuous, sometimes extensive alteration, chiefly in favor of the land, and the stenotopic riparian fauna has led an extremely unstable existence. The occurrence of relicts in former coastal regions would be easily understandable. Concerning the presumed coastal relicts of the flora, see Elsa Warburg (1910, p. 166).

Occurrence along the shore can probably be thermally determined, as in the case of *Nebria gyllenhali* (p. 685) in the negative direction, and in the case of *Bembidion assimile* probably in the positive direction. The former was therefore described as a "cold relict." However, in general it is not possible to decide whether thermal, hygric, edaphic, or other factors are decisive for the more or less marked association of a species with the seashore, so that the neutral term "coastal relict" may be appropriate.

The following species, whose main occurrence is on the seashore (or at least in coastal regions), also have inland localities—mostly at the larger lakes—which deserve to be investigated from the viewpoint of the relict hypothesis:

Bembidion assimile	*Dromius linearis*
B. pallidipenne	*Dyschirius impunctipennis*
Cicindela maritima	*D. obscurus.*

695 It is first important to emphasize, that in none of these species is there any dependence on NaCl of the sea. In the case of *Bembidion pallidipenne* and the two species of *Dyschirius* "halophily" was assumed; but this is no doubt purely edaphic (due to the occurrence of suitable sand) and does not deserve any such name (p. 524). Two of the other species are also sand-dwelling insects, but *Bembidion assimile* is associated with loam. We are justified in arguing that these 6 species have achieved a largely coast-bound distribution, first due to edaphic factors, second due to the highly favored possibilities of immigration along a more or less uniform coastline. Climatic factors may also have been effective.

Krogerus (1932, pp. 248, 252) analyzed some Finnish inland localities of *Cicindela maritima* (Kb Kontiolahti, Sb Kuopio) and *Dyschirius obscurus* (Kb Kontiolahti)—both stenotopic quicksand species—and provided a map illustrating the striking position of these localities along the shoreline during the maximal transgression of the Ancylus Lake. There is no doubt of a casual connection here. In the case of *Dyschirius obscurus*, all the Finnish inland localities of records are situated below the highest postglacial shoreline (Magnusson

and Granlund, 1936, p. 179; Sauramo, 1942, p. 229) and can be considered as coastal relicts. Even in the case of the only Swedish inland locality, Hll Vessige, Sjönevadssjön (58.5 m above sea level), this was so at least during the Baltic Ice Lake period; however, it is uncertain whether the species had immigrated that early. *D. impunctipennis*, occurring at Lake Ladoga, where the only enduring inland-lake populations in Fennoscandia are found, may likewise be considered a coastal relict.

The other 4 species (including *Cicindela*) cannot be coastal relicts throughout northern Europe (including Denmark and the eastern Baltic region). They occur in postglacially constantly supraaquatic regions:

Bembidion assimile near Små Bolmen, in Denmark, and in the eastern Baltic region.

B. pallidipenne on two lakes of Jutland (and in Holstein);

Cicindela maritima in central and northern Norway; also in the eastern Baltic region;

Dromius linearis in Denmark.

However, in support of the contention that these species too are partly coastal relicts, the following facts may be added:

Bembidion assimile. On the large central Swedish lakes this species also occurs in the brachypterous form—which even predominates. In this form it is not easy to migrate by fits and starts (cf. p. 393). On the other hand this is also true for Bolmen in Små, a lake which never had a postglacial connection with the open sea.

696 *B. pallidipenne*. All of the three Swedish inland records (in Skå) lie below the highest shoreline (see Munthe, 1940, Plate II).

Cicindela maritima. Even the localities in the northern Finland lie below or at least in the immediate vicinity of the highest shoreline; in Sweden all of the localities are situated below it.

Dromius linearis. The only two Swedish localities, situated at a considerable distance from the sea, are on the shores of lakes Vänern and Vättern. Near Ögl Motala, the species is constantly endemic, here as far as is known, only in the brachypterous form, as also near Vgl Kinnekulle (1 specimen).

D. "Anti-culture Relicts"

For lack of a better name we here so designate species that seem to have been so badly affected by human culture that they remain as relicts only in part of our region virtually untouched by man. As possible examples, *Agonum bogemanni, Amara nigricornis* and *Harpalus nigritarsis* were mentioned above (p. 636) as "decreasing species." Perhaps the extremely isolated Norwegian locality of *Agonum mannerheimi* (12 Vardal) is to be similarly interpreted; it is a definite "species of virgin forest." *Agonum bogemanni* and *Harpalus nigritarsis*, probably also *Trachypachys zetterstedti*, seem to be in process of be-

coming extinct throughout the Fennoscandian region. It is uncertain whether the restriction of the small, homogeneous, isolated area of *Agonum longiventre* to the lower reaches of the Dalälven River is partly due to human culture as well (cf. p. 720).

I am not in a position to decide whether in any of these cases extinction from "internal causes," such as "the degeneration of an old species" may be involved.

E. Interglacial Relicts

Included in this category are animals and plants that lived in Fennoscandia during the last interglacial period and were not completely expelled by the subsequent glaciation (Würm), but displaced in their distribution—chiefly toward the Scandinavian west coast. The best-known example in our fauna is the fjeld lemming (*Lemmus lemmus*: Ekman, 1922, pp. 397 ff.).

697 Some of the (established or presumed) interglacial relicts have again expanded their area in the postglacial period to the extent that their relict character has been lost, especially when they have merged with the stocks that immigrated from outside the Fennoscandian region. In others, the spatial separation of the Fennoscandian interglacial stock is still sharply distinct.

This phenomenon cannot be categorized with the "cold relicts." All of the species in question have rather the opposite, no pronounced need of cold and they were not favored, but adversely affected, by the enduring glacial period.

Basic to the formulation of our problem is the question how far the present-day Fennoscandian fauna originated from interglacial relicts. Hence the last section of this book is devoted to this question.

Perhaps the abiding impression of this section is that I have handled the relict concept somewhat casually, since here the category covers populations not clearly isolated on the map. However, the most important characteristic of a relict is not the space factor but the *time factor*.

698

The Postglacial Immigration

The two preceding sections are designed as useful preliminary exercises for describing postglacial faunal history. The fossil records ought to teach us that no definite conclusions as to the prehistoric areas of species can be drawn from the present-day distribution alône. The relicts primarily show that the postglacial "migrations" of organisms do not represent any methodical striving in definite directions, but pulsating, intermittent area displacements, which—even if verifiable—often remain unexplained. With all their commendable clarity the maps on the recent and prehistoric distribution of *Hippophaë rhamnoides* (Sandegren, 1943) show how impossible it is in some cases to give a reliable judgment on the postglacial history of an organism based on the present-day area of the species. This is of course an extreme case, the example of an especially noncompetitive plant, which has no counterpart at all among the animals considered in the present contribution. However, the warning reminds us to exercise caution in cases where the recent picture presented by the map is the only available basis of historical discussion and conclusions.

An essential precondition for understanding the postglacial history of the fauna and flora of Fennoscandia is a knowledge of nonbiological features, especially within two branches of study: the late Quaternary climate (including the condition of the terrestrial ice) and the distribution of land and water during different periods, some of which go far back in time. No attempt is made here to provide a cogent glacial and postglacial history of Fennoscandia in respect of these. The information in these fields, necessary for an understanding of the faunal development, is given below in the relevant context. However, Table 36 (p. 661) gives a synoptic representation of the development of the
699 late- and postglacial climate. The concurrent changes in the distribution of land and water are illustrated here in four maps taken from Granlund (Magnusson and Granlund, 1936) (Figs. 97–100).

Right away it must be conceded that the authors are not at all unanimous about the climatic development or the development of different stages of the Baltic Sea. As a layman, with no primary knowledge in these fields confronted with strikingly divergent opinions, it was sometimes very difficult for me to decide which view was the more plausible. And the decision was perhaps too

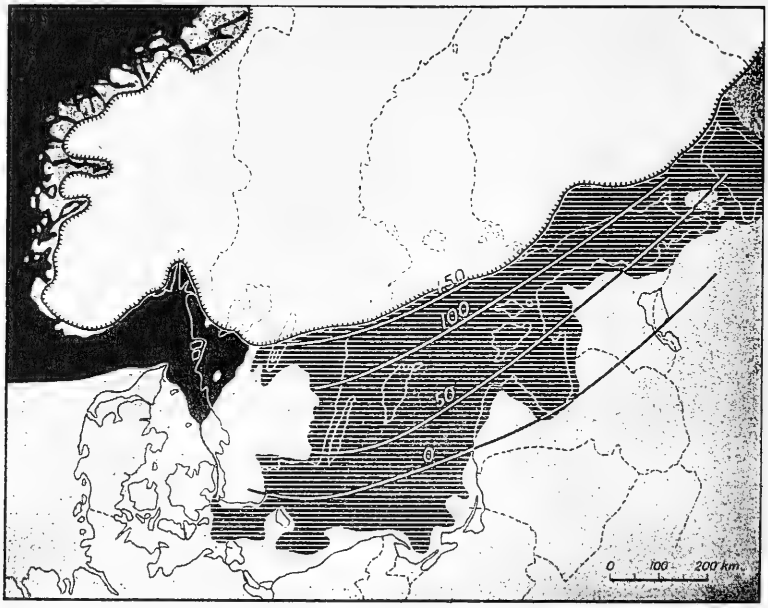


Fig. 97. Baltic Ice Lake (hatched). According to Granlund (1936).

often based on the democratic but superficial principle of the majority.

As an example of biogeographically important details of Granlund's maps that are otherwise conceived by other researchers, mention may be made of the following: Munthe (1940, e.g. Plate III) assumes that occasionally salt water forced its way through the Danish straits into the Blatic Ice Lake (also considered probably by Ekman, 1930, p. 239). His view (e.g. Plate XI)—shared
700 by some other authors—that Öland was firmly connected with Småland during part of the Ancylus period, does not find expression in Granlund's map. Sauramo (1942) shows Bornholm as completely submarine both during the time of the Baltic Ice Lake (p. 227) and during the Ancylus period (which conflicts with his own isobases). For the Littorina period (pp. 239, 241) he does not assume any open connection between Lake Ladoga and the Gulf of Finland, and substantiates his concept with a shore curve of Ik Ino (p. 242). Concerning the question whether a postglacial sea connection existed between the Gulf of Finland and the White Sea, see below (p. 730). Supra-aquatic land between Öland–Gotland and Pomerania is assigned by Granlund to the Ancylus period, by Munthe (l.c.) to part of the Baltic Ice Lake period and the early Littorina period as well. This question has been considered above (p. 308), where a firm land connection of the two above-mentioned islands southward was considered so to speak a biological necessity.

It is a matter of prime importance how far biogeographers are justified

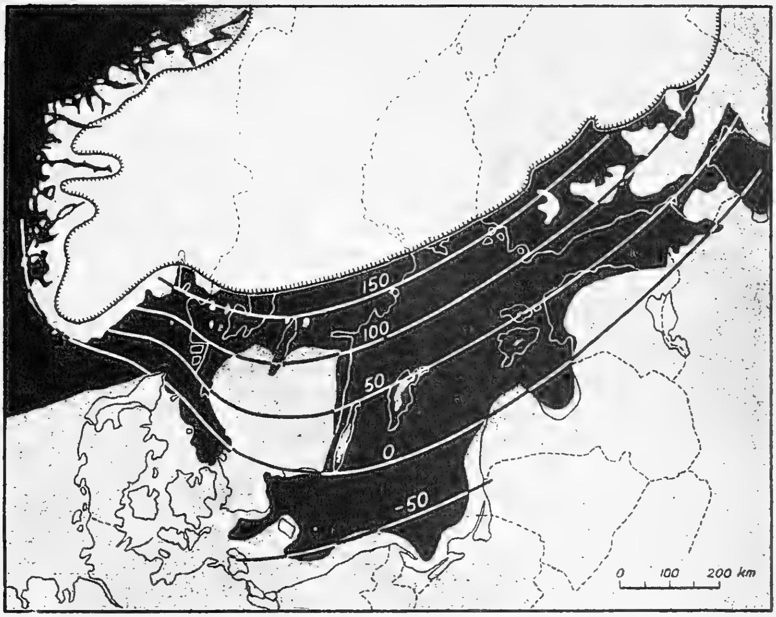


Fig. 98. The Yoldia Sea. According to Granlund (1936).

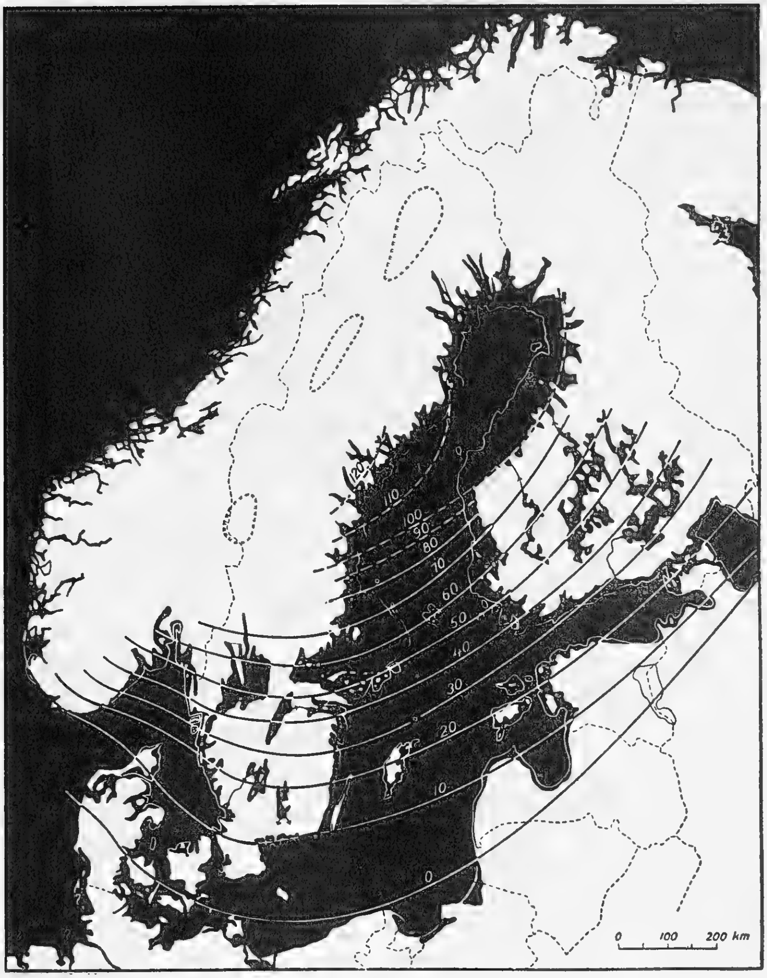
in passing judgment on prehistoric land connections, climatic conditions, etc.,
701 which have not been clarified by the specialists concerned, perhaps not even
discussed. Tanner (1937, pp. 101, 107) thinks that, for instance, the "problem
of hibernation" of the flora and fauna of Fennoscandia and other regions must
be solved by geologists, and attaches little value to conclusions arrived at purely
702 biogeographically. Typical of his approach is the discussion on the history of
the flora of Labrador (1944). With respect to numerous facts cited especially by
Fernland in favor of a hibernation of plants in Labrador refuges during the last
glaciation, he denies this possibility, "as the whole of Labrador is presumed
to have been covered with ice during the Wisconsin [=Würm] glaciation"
(p. 356). He of course earlier (pp. 174–175) conceded that so far it had not
703 been possible to divide the glacial deposits of Labrador into different glacial
epochs; all of them—"for logical reasons"—are included in the last glaciation!

The ideal researcher would of course be one competent to work in nature both biologically and geologically; Nordhagen comes very close to this ideal. However, it is unreasonable when the geologists deny the right of the biogeographers to interpret the biota history purely on the basis of biological material. They cannot deny that biogeographical conclusions, for instance, with respect to the glacial conditions in the western Scandinavian coastland, can provide and indeed have provided valuable impetus to geological research, as well. On

701 Fig. 99. The Ancylus Lake (hatched). According to Granlund (1936).

the other hand it is important that the biogeographer familiarizes himself with current geological (paleoclimatological, etc.) ideas and—within reason—feels bound by them. He must be able to cite an entire series of facts before questioning the relevant views of another special science. The proclamation of land connections and other geomorphological upheavals on the basis of the distribution of a single species of animal (for example, Ihering, 1927, p. 220) is quite wrong and only discredits the whole of biogeographical science.

The position of Fennoscandia on the northwestern corner of a continent



702 Fig. 100. Littorina Sea at the time of maximum extension. According to Granlund (1936).

shows that its postglacial recolonization was possible from two main directions, south and east. Therefore and on account of the unusually effective destruction of biota even by the last glaciation (Würm), Fennoscandia offers an especially suitable field of research on the most recent history of fauna and flora which has few counterparts anywhere in the world. The problem is complicated by the greater or lesser importance attached to the possibility of "hibernation" of the biota during the Würm period—or even during earlier glaciations; and

of course even these problems in our region are far simpler than, for instance, in the central European mountains.

An account of faunal history is therefore logically divisible into three groups of species:

I. The southern postglacial immigrants;

II. The eastern postglacial immigrants;

III. The hibernation group, which is predominantly western.

704 Doubts may arise in certain cases whether an immigration group is to be considered as eastern or southern. I have preferred to proceed so to speak nationalistically, from Sweden. I call all manifestations of immigration from the other side of the Baltic Sea "eastern," even the group that has invaded Finland directly from Estonia across the Gulf of Finland, which, seen from Finland, is "southern." Similarly, species that have reached southernmost Norway (southwestern Norway) directly across the sea are to be considered as "western." However, no special section is devoted to them, since this involves the important and difficult problem of separating them from the "hibernators." This "western" group, whatever its assumed origin, is therefore treated in the concluding section devoted to the question of hibernation.

I. THE SOUTHERN IMMIGRANTS

The first precondition for correctly visualizing the postglacial (*s.l.*) immigration of plants and animals from the south—from Central Europe—is to ascertain the initial stage, the faunistic character of Europe south of the Nordic ice margin during the Würm period.

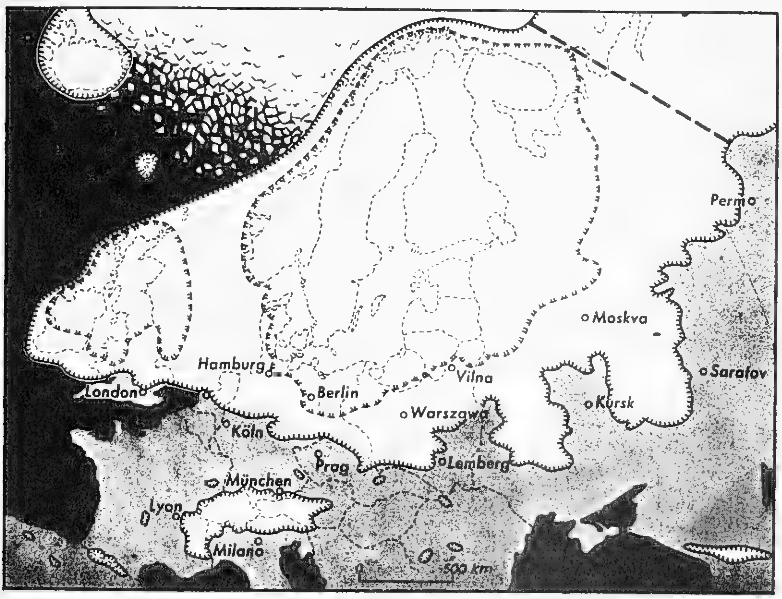
It is well known that the uninterrupted ice cover during the last glaciation (Würm) was much less extensive than during the great glaciation preceding it (Riss) (Figs. 101, 102). The difference was greatest in the west and, especially in the east, whereas just south of Sweden, in northern Germany, the distance between the southern edges of the Nordic inland ice during the Würm and during the Riss scarcely exceeded 150 km.

Thanks primarily to the studies by Henriksen (1933) on the subfossil fauna of Denmark and Skåne we are well informed about the coleopteran fauna, which during the Würm Ice Age lived in the immediate vicinity of the southern ice edge and hence represented the first immigrated "southern" element in Scandinavia. There are 15 species of carabid from the "late glacial" deposits of these regions (see list of fossil species above, pp. 665 ff.). Of these, 10 live in the present-day *Regio alpina*, one has apparently become extinct (*Nebria fossilis*), only 4 are unknown above—and north—of the *Regio coniferina* (*Agonum*
705 *dolens*, *A. viduum*, *Bembidion repandum*, *Chlaenius costulatus*; *Agonum viduum*, which was not studied by Henriksen, is probably doubtful). The high Nordic character of this fauna is best shown by the fact that of the meager 5 carabid species actually native to the Fennoscandian higher *Regio alpina*, only one

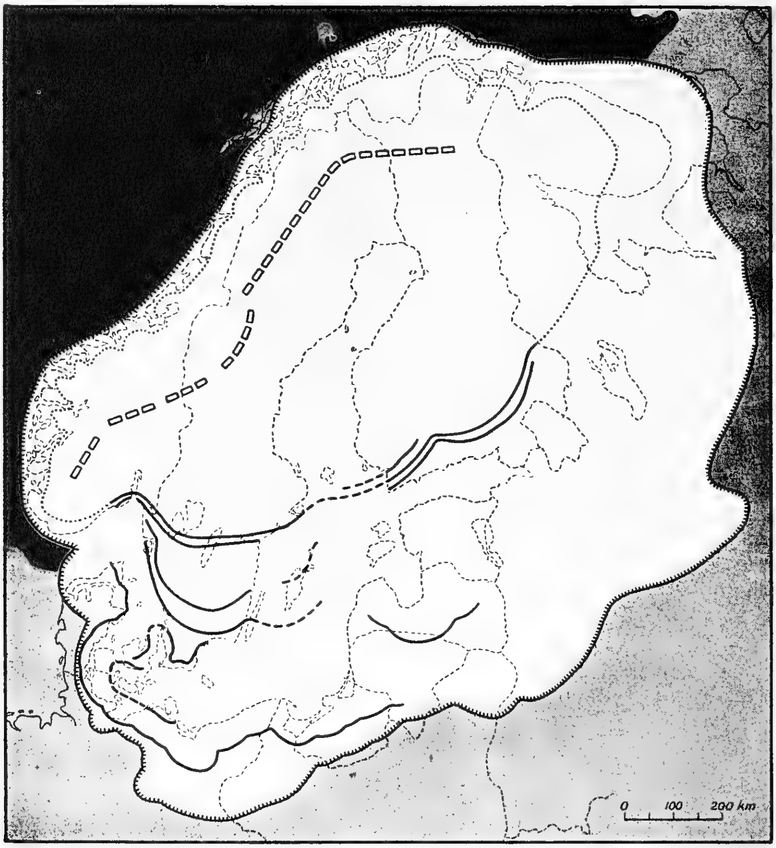
species (*Nebria nivalis*) is missing from the material (species represented are: *Amara alpina*, *Nebria gyllenhali*, *Notiophilus aquaticus*, *Patrobus septentrionis*; see Table 30, pp. 440 ff.).

The same fauna undoubtedly accompanied the southern edge of the maximal Würm ice, even in Central Europe. Various subfossil "glacial faunas" are actually known from these regions (Nathorst, 1894; Lomnicki, 1894, 1914; Schille, 1916), but it does not seem possible at present to decide whether they actually lived contemporaneously with the *last* glaciation. In any case, here we are interested in the question in how near to the Würm ice lived a richer
706 fauna that included such species too which in present-day Fennoscandia do not normally cross the timber-line.

In this respect the entomological subfossils seem to leave us in the lurch, and we must have recourse to a more reliable science, the pollen analysis. There are of course few precisely dated samples from Central and Southern Europe, but these give an approximate idea of the pattern of vegetation there at the time of the Würm maximum (Fig. 103). From these facts, Firbas (1939) concludes that during the Würm maximum there was only a local *Betula-Pinus*



705 Fig. 101. Maximum ice cover during the penultimate (Riss) and the last, lesser (Würm) glaciation. Local glaciations in Central European mountains are generalized and indicated only for the Riss. According to Granlund (1936).



706 Fig. 102. Last glacial period (Würm) in northern Europe: Position of ice edge during some phases of recession indicated. According to Granlund (1936).

707 flora—corresponding to the present-day *Regio betulina* and *Regio coniferina* of Fennoscandia. It was confined only very locally mainly to the west, in the ice-free belt between the Nordic and Alps ice, becoming richer only south of about 48°N. Forests with "heat-requiring trees" (corresponding to the *Regio quercina* and *Regio fagina*) seem to have "hibernated" only in the Mediterranean region.

These considerable distances in north-south direction between the plant regions of the Würm period were apparently made up relatively quickly after the melting phase set in. At any rate the forest-forming *Betula* and *Pinus* were already in Skåne at the end of the Baltic Ice Lake period (v. Post, 1933, p. 58; T. Nilsson, 1935, pp. 468 ff.; Magnusson, 1936, p. 237), when the ice edge was

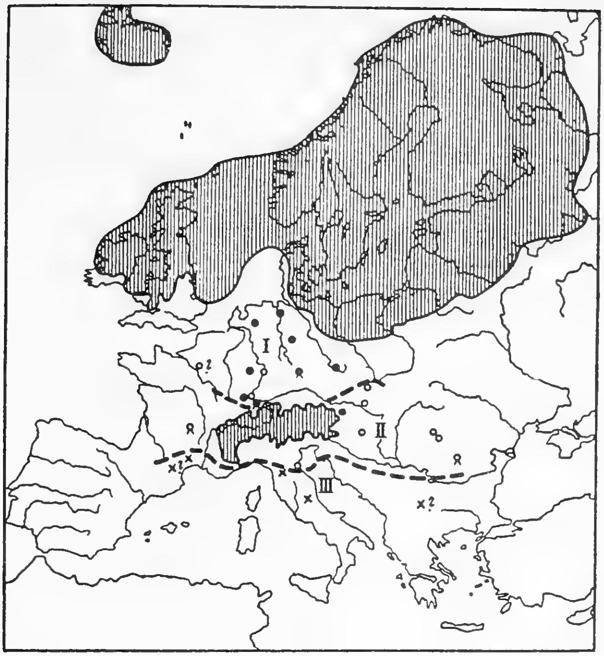


Fig. 103. European vegetation zones during the last glacial period (Würm). Black points: glacial flora without trees. Blank points: *Betula* and *Pinus*. Crosses: "heat-requiring trees." According to Firbas (1939).

still present in northern Götland, and "true" deciduous trees already existed
708 at the end of the Yoldia period. Despite the much greater distances from the assumed hibernation regions, in their migration northward to Scandinavia the more heat-requiring elements were thus not far behind the species of the tundra (*Regio alpina*).

However, the first southern immigrants were tundra species. In classifying the Fennoscandian fauna in its larger historical context it is of great interest to establish whether the species of this first immigration group originated from a true "mixed fauna," ("Mischfauna")†, which arose in the ice-free Central European belt during the Würm period as a conglomerate of Nordic and Central European interglacial montane faunas, or whether the Scandinavian or the alpine fauna emanating from the Alps (and other mountainous regions) during the Würm period, each stayed chiefly along "its" local ice edge. I have already considered the problem (Lindroth, 1935a, p. 626) and cited the following facts.

†(Suppl. scient. edit.).

The late-glacial coleopteran fauna in Denmark-Skåne (according to Henriksen, 1933) includes 6 or 7 Nordic species, which are absent from Central Europe today:

Amara alpina	*Colymbetes dolabratus* Payk.
Bembidion hasti	*Thanatophilus lapponicus* Hbst.
Elaphrus lapponicus	*T. trituberculatus* Kirby
Agabus serricornis Payk. (determination uncertain)	(= *Silpha baicalica* Mtsch.).

Bembidion repandum, which is known in Central Europe only by one specimen from Jutland, should also be included here.

The Nordic origin of this group is now more evident since no fewer than 4 of the 7 species (the three carabids plus *Colymbetes dolabratus*) were found in *interglacial* deposits in Sweden (Lindroth, 1948a)*.

In contrast with this group there are (in Henriksen's material) only two species from the Central European mountains, which are alien to present-day Fennoscandian fauna:

709 *Bembidion ? glaciale* Heer   *Simplocaria deubeli* Ganglb.

Of these, *Bembidion* is definitely high-alpine (for example, Heberdey and Meixner, 1933, p. 70), whereas *Simplocaria* is an animal of subalpine forests (Ganglbauer, 1904, p. 61).

Hence from the deposits along the southern edge of the nordic Würm ice we know at most one true "alpine"** species (*Bembidion ? glaciale*), today missing from Fennoscandia, as against the 6 or 7 nordic species, unknown in Central Europe. And indeed the alpine fauna of the Alps is incomparably richer than that of Fennoscandia!

"It is tempting to explicate these facts in the following way. The northern Würm-ice did not extend southward far enough (viz. the ice of the Alps not northward) to make a 'Mischfauna' of northern and southern elements (especially not of their most cold-requesting forms) possible. The alpine and subalpine species therefore, after the Würm ice had begun to retreat, returned mainly the same way by which they had come, to the north or to the south, an exchange taking place to little extent only" (Lindroth, 1935a, p. 627). According to the map by Firbas (1939) (Fig. 103) it cannot be ruled out that a narrow zone of *Betula-Pinus* forests even at the Würm maximum represented a kind of barrier for true alpine organisms. The great faunal and floral exchange

*This is also an important proof that the occurrence of these species in late-glacial deposits cannot be explained by immigration from the east (from Russia or Siberia) along the Würm ice edge. On the other hand this could be true of *Bembidion repandum* and, *Thanatophilus trituberculatus*, and probably also of *Chlaenius costulatus*.

**The term "alpine" here and in the subsequent discussions indicates an inhabitant of the *Regio alpina* and does not carry any geographical implication.

that led to the emergence of the boreo-alpine type of distribution may have occurred by all means not during the Würm but during the Riss Ice Age (as already assumed by Brundin, 1934, p. 172).

Let us now consider more closely two questions concerning the southern postglacial immigration to Scandinavia:

a. To what extent did the first immigrating alpine and subalpine species manage to reach the Fennoscandian mountains, to become resident there?

b. Whatever their climatic requirements and time of their first arrival—how far north have members of the group that immigrated from the south reached?
710 Or: How large a percentage of the area of today's Fennoscandian fauna is accounted for southern immigrants which arrived through Sweden?

a. During the initial stage of the melting of ice the possibilities of immigration to Skåne through Denmark were highly favorable for alpine—eventually also for subalpine—plants and animals, not only on account of the nearly or completely uninterrupted land connection between these regions during the Baltic Ice Lake period but also because the ice retreated here at only moderate speed (about 50 m per year; Granlund, 1936, p. 235), so that fairly stable biotopes were formed. In line with this the localities of subfossil alpine plants in the southern half of Skåne are more numerous than anywhere else in Sweden below the fjelds (Granlund, 1936, p. 239). Postglacial subfossil finds of alpine or subalpine insects in Sweden have solely been made in Skåne.

The extremely sparse subfossil finds of true alpine organisms in Sweden north of Skåne have been interpreted by several authors as an indication that in these regions the alpine fauna and flora apparently encountered various barriers, blocking or impeding their dispersal northward (Ekman, 1922, p. 374; Brundin, 1934; p. 196; Lindroth, 1935a, p. 625; Nannfeldt, 1935, p. 77; 1947, pp. 75, 77). At first the melting of ice proceeded relatively slowly, which indicates only moderate climatic improvement on the average; it took the ice edge more than 4000 years to move from southern Skåne to Vgl Billingen (see Table 36, p. 661), so that on the average a strip of just 80 m of land was freed each year. However, hereby the ascertained fluctuations of the ice edge in Skåne (for example T. Nilsson, 1935, pp. 471 ff.), are taken into consideration and it is fairly certain that the ice melted faster north of Skåne (up to Billingen). So we are already led to surmise, especially for the much faster melting phase of the central Swedish moraines (and the Salpausselkä of the same age in Finland) up to the point of bipartition in Jtl—i.e. the finiglacial period (in De Geer's sense)—that the forest immediately succeeded the retreating ice, and no space was left for a real alpine vegetation. This view easily leads to
711 mistakes. Even if for climatic reasons the *Betula-Pinus* forest was able to follow up the ice edge, the receding ice must have been accompanied by a forest-free zone—if only because of the slow growth of young trees; the faster the ice retreated, the broader this zone. According to the above (minimal) shift of the ice edge of southern Sweden, 80 m per year and on the assumption that

saplings must be at least 3–4 years old to exercise any influence on the other vegetation, we get a 200–300 m "forest-free" zone along the ice edge. In the Stockholm region, where an average early ice recession of 250 m per year has been established (De Geer, 1940, p. 97), this zone attained a width of almost 1 km. It is somewhat paradoxical: the faster the ice receded, the larger the woodless area available for alpine plants. They were evidently endangered by the forest in a different way: its advancement at the same speed as the ice receded imposed on the organisms dependent on open biotopes a constant, equally fast displacement, which badly affected perennial plants with poor capability of dispersal (like most of the fjeld plants). For the same reason it is conceivable that the high temperature of the macroclimate, already evident during the "Subarctic" period, had this effect on the coldrequiring plants that found microclimatically suitable places for germination close to the ice; but in subsequent years these places had already changed so unfavorably that the perennial plants never reached the stage of bearing fruit. However, this holds only to a very limited extent for actively mobile animals, as well as for annual and biennial plants. I therefore believe that the absence of alpine-subalpine subfossils from central and northern Sweden outside the fjeld regions, and the slight importance we need attach to the "southern" immigration route of such organisms, are not due only to the rapid melting of ice.

The standstill period of the ice shortly before and during the Yoldia epoch may have been far more fateful for the alpine fauna and flora. With regard to the duration and the exact conditions of this stage—especially with regard to the isolation of the Baltic Ice Lake—there are of course widely divergent views (Lundqvist, 1946, pp. 281 ff.). But it is clear that the retreat of the nordic inland ice at the latitude of the Billingen mountain in Vgl (and simultaneously near
712 Salpausselkä) was interrupted for a period whose duration has been estimated by various authors at 650–800 years (Granlund, 1936, p. 155; Munthe, 1940, pp. 63–64). At first thought one would be inclined to take such a standstill period of the ice as advantageous for alpine plants, during which constantly cold biotopes were formed along the ice edge. But it looks as if such a stage did not arise—at least not exclusively—as a result of a decline in temperature, but as a result of increased winter precipitation (Hyyppä, 1933, pp. 29 ff.; 1936, pp. 446 ff., 458; Sauramo, 1942, p. 281). A general oceanization of the climate could also explain the apparently simultaneous increase of birch at the cost of pine in Central Europe (Firbas, 1939, p. 87). It can easily be visualized that, if this view is correct, the forest in central Sweden would have quite caught up with the ice edge.

Of course these questions on climate are not to be considered as decided. It is quite possible that the so-called late Dryas period (for example in Thomasson, 1935, p. 615) coincides with the standstill of the ice edge.

Still more destructive may have been the effect of the altitude on the alpine organisms that had immigrated from the south. The ice edge was stationary

for a long time over the Billingen mountain, but as soon as it retreated* from its northern edge, an open connection appeared between the Baltic Sea and the ocean. The Yoldia period set in, and on account of the depressed position of the central Swedish plain, the ice edge lay for 400–500 years milking in the broad Närke Strait, which in the beginning contained only a few, smaller islands. Even if the distances across the Närke Strait were not insurmountable for plant diaspores and flying animals, there was almost no inhabitable land at all on the southern edge of the inland ice. The alpine flora and fauna—to the extent that they had generally followed the ice—remained "stationary on the southern shore of the Närke Strait," slow victims of the warmer climate and the advancing forest. It is thus no accident that the northernmost Swedish record of subfossil alpine plants (*Arctostaphylos alpina*, *Dryas octopetala*) was made outside the fjelds near Nke Laxå (G. Andersson, 1906, p. 60; v. Post,
713 1909, p. 694), in the immediate vicinity of some small supra-aquatic regions which emerged as islands in the early stage of the Närke Strait (see map, Plate II, in Munthe, 1940).

Ekman (1922, p. 412) thinks that birds, flying insects and possibly small animals with especially strong passive capability of dispersal belonging to the "purely arctic" fauna may have been able to migrate along the Swedish west coast in the late-glacial period and, following the ice edge in southeastern Norway, reached the present-day *Regio alpina*. Wahlgren (1913, p. 143) originally held a similar view with regard to certain alpine Lepidoptera (but he had in mind immigration to Norway from the southwest across the sea). Later (1919, p. 25), however, he classified this element as Würm-hibernating. Actually the possibilities of a migration or passive transport of alpine organisms during the critical period (at the end of the Baltic Ice Lake period, the beginning of the Yoldia period) across the sea from the Danish-southern Swedish mainland to southeastern Norway were still poorer than across the Närke Strait. The distance was greater and the higher salt content of the sea militated against hydrochorous or anemohydrochorous transport (p. 600).

We thus conclude, that the pronounced alpine-subalpine fauna, which demonstrably lived along the southern edge of the Würm ice at the time of its maximum, and in Denmark-Skåne formed the first colonizers, at the most reached the southern shore of the Närke Strait. Relicts from this period, of those mentioned above (p. 682), may be at least *Pterostichus adstrictus* in Små and *Nebria gyllenhali* and *Patrobus assimilis* on Gtl, the first of these also on the Vätter Lake; from all these regions there are subfossil finds of true alpine plants. Likewise *Pinguicula alpina* and *Bartsia* in Gtl, *Viscaria alpina* and *Poa alpina* in Öld, etc., have generally been considered as late-glacial

*It is still contested whether this "isolation" ("Zapfung")† of the Baltic Ice Lake was at once definitive, or whether it was repeated by oscillations of the ice margin (Lundqvist, 1946, p. 282).

†(Suppl. scient. edit.).

relicts. I find this explanation also applicable to the occurrence of *Alchemilla alpina, Rhodiola rosea* and *Viscaria alpina* in western Sweden (even if they are "pseudorelicts"; cf. Nannfeldt, 1935, p. 77). The occasional suggestion that they wandered down from Norway during a later cold period (for example Sernander, 1894, p. 200) is most unlikely in light of the southern Swedish inland finds of *Alchemilla alpina* (map in Lid and Zachau, 1929, p. 97). But none of the above-mentioned species of beetles and plants is markedly alpine
714 or even alpine-subalpine (i.e. with the normal lower limit along the coniferous timberline), so they do not show that the most cold-requiring forms of the late-glacial deposits from Denmark-Skåne reached just as far north.

We will return (p. 765) to the question whether the alpine and other species were able to immigrate to southern Norway directly across the sea.

b. It is often easy to determine how far north the stock that immigrated across southern Sweden has advanced if it is geographically (and functionally) distinct from the almost obligatory stock on the other side of the Baltic Sea and there is no reason to assume a western (or northern) interglacial element. A series of examples of such species was cited* above (p. 618) and their collective northern limits were cartographically represented (Fig. 82) groupwise—according to the position of this limit in Sweden.

Evidently, at least a limited number of species reached the provinces of Nbt and Vbt by immigration across southern Sweden. However, where the Swedish area extends up to the Finnish border on the River Torne-älv, the origin is more uncertain. Practically without exception the area then continues uninterrupted to the other side of the border of the kingdom right across Finland. Simultaneous immigration from the south took place on both sides of the Gulf of Bothnia. The two stocks have merged. Is it possible to decide in such cases whether this happened on the Swedish side or on the Finnish side?

In some cases such a reconstruction is in fact possible. We proceed from species in which the Swedish stock and the Finnish stock have still not met in order to ascertain the position of the gap between them. In most cases neither of the two stocks has reached the northern end of the Gulf of Bothnia. Then the northern limit is usually highest in Finland. Doubtless, the situation is often climatically determined and is to be explained (p. 459) by the average higher summer temperature at a given latitude in the inland of Finland.

715 In a series of cases mentioned below (p. 734) the Finnish stock has, however, reached the northern end of the Gulf of Bothnia and crossed the border of the kingdom, which the Swedish stock has failed to do, so that on the Swedish side there is a more or less broad gap. This situation can in no way be attributed to present-day climatic conditions.

*The selection above (p. 618) was not made from the viewpoint of the immigration route. There some species, whose exclusively southern origin is uncertain, were included among the species that advanced farthest north (as far as Nbt). In the latter context the following "Nbt species" are probably u..ambiguous: *Agonum versutum*, *Amara ingenua*, *Cicindela campestris*.

The question arises whether—in the name of justification—there is a converse group whose members have advanced farther north in Sweden, i.e. have encroached into the Finnish region, and are separated by a more or less distinct gap from the southern Finnish stock. We find at the most 4 species of which this might be true:

Agonum micans	*Carabus violaceus*
A. versutum	*Synuchus nivalis.*

Further analysis reveals:

Agonum micans is a very late immigrant (p. 632, Fig. 87) in both countries—at any rate in the north—and the map is to be considered incomplete. If we must explain this it seems more probable that the stock arrived at the northern end of the Gulf of Bothnia from Finland (through Kuusamo), and not the converse.

Agonum versutum has just one locality in Finland (Ob Ylitornio) along the River Torne, which is connected with the Swedish area. The encroachment into the Finnish region is thus as meager as possible.

Carabus violaceus. That the Finnish population north of latitude 64°N arrived from the west seems very probable from the map. Moreover, in northern Finland the "*arcticus* form" might occur without smooth transition to the southern type (as in Scandinavia) (Hellén, 1934, p. 45). Yet this species does not fit our problem as an example. It undoubtedly belongs to the Würm hibernators on the Norwegian coast, and the northern Finnish stock certainly did by no means come from southern Sweden.

Synuchus nivalis. The locality Ob Kemi, very isolated from the rest of the Finnish area, historically belongs to Sweden beyond doubt.

As as counterpart to the above-mentioned 17 species (p. 734) emanating from the east there seem to be only 2 species (*Agonum versutum, Synchus*) that reached the northern end of the Gulf of Bothnia apparently by moving up through Sweden, including the nearest part of Finland.

716 In species with *wing dimorphism* it is often possible, even after two immigrant stocks merged, to determine the "cicatrice" as a zone with strikingly numerous macropterae. In this way we found above that in *Bembidion guttula* (p. 387 and Fig. 42), *Carabus clathratus* (p. 381 and Fig. 38), *Pterostichus lepidus* (p. 381 and Fig. 37), *P. minor* (p. 387 and Fig. 43) and *P. strenuus* (p. 395 and Fig. 47) *only the Finnish stock* reached the northern end of the Gulf of Bothnia. The only conceivable—but uncertain—contrary case would be *Bembidion lampros* (p. 382 and Fig. 40), of which it can probably be argued that it also invaded the southern fjeld regions of Sweden by direct immigration from the south.

The above discussion therefore confirmed the view earlier expressed (Lindroth and Palm, 1934, p. 127) that the fauna of the upper Swedish north coast acquired its character mainly by the northeastern immigration group. The unambiguous southern immigrants—even among the remaining Coleoptera—are

astonishingly few in these regions. There are corresponding conditions for the flora: “the number of species around the Gulf of Bothnia that have come from Sweden is very small” (Cajander, 1921, p. 6).

One may justifiably ask whether on the rugged western Scandinavian coastal region, in Norway, the possibilities for the advancement of a stock that immigrated from the extreme south across Skåne have not been still lower, and whether it can be supposed that such immigrants colonized regions north of Tröndelag in the postglacial period (Provinces 26–28).

However, a verification does not quite draw blank. The following species, which in Norway reach at least latitude 64° N, must be considered as immigrants across southern Sweden:

Agonum assimile	*Bembidion dentellum*
A. mülleri	*Dromius fenestratus*
A. viduum	*Harpalus aeneus*
Amara ingenua	*H. pubescens.*

Probably also to be included is *Amara familiaris*, which in Norway has advanced even beyond latitude 69° N. So has *Calathus erratus* and the map on dimorphism (Fig. 35, p. 376) clearly shows its southern origin. The migrations were greatly facilitated by the passes between the Oslo and Trondheim re-
717 gions, which were much more favorably situated in the warm period. Namely the flying species could have reached the Norwegian coast from Sweden directly via the northern passes, as was mentioned earlier (pp. 614 ff.). But the small number of these migrants is remarkable. In the Norwegian fauna north of Tröndelag the component of the species that immigrated across southern Sweden is of very little importance.

It needs to be emphasized that the species that immigrated from the south across Denmark-Skåne did not always advance on a broad front along with the northward moving northern boundary of the west-east limit running across southern Sweden. At the beginning even more than today, the southern Swedish highland represented a climatic obstacle. The edaphically fastidious species, for example, loam-bound species, were excluded thereof. Because there is little loam along the east coast of Småland (Fig. 78, p. 511) for many species it was possible to bypass the highland only in the west. The characteristic animals of the central Swedish warm and loam region immigrated chiefly from the southwest, across the plain of Vgl. This feature is evident from the dimorphic map of *Bembidion assimile* (Fig. 46, p. 394) and in *B. aeneum* (Fig. 49, p. 400; Fig. 80, p. 521). Other examples are *Agonum marginatum, A. moestum, A. thoreyi, Bembidion articulatum, B. illigeri, Dyschirius lüdersi.* It is quite possible that the isolates interpreted as relicts of a number of species, chiefly in the Mälar lake region (p. 691), originated, at least partially, by immigration from the same direction.

Finally it must be remembered that "southern" immigration into Scandinavia also took place by routes other than Denmark-Skåne, partly in the southwest across the sea to Norway (see p. 765), partly, and chiefly, to the large Baltic islands. In the latter case the assumption of an early postglacial land connection with northern Germany seems to be necessary (pp. 308 ff.). It is very difficult to judge how far this immigration route also had a role in colonization of the Swedish mainland.

718 II. THE EASTERN IMMIGRANTS

The eastern marginal regions of Fennoscandia, compared with the corresponding regions of Scandinavia, were free from Würm ice astonishingly early. Already at the end of the Baltic Ice Lake period, when the ice edge coincided with the central Swedish moraines and Salpausselkä*, the whole of eastern Karelia, the Kola Peninsula and the adjacent parts of Finland were ice-free (Sauramo, 1942, map on p. 227). Immigration of plants and animals on a broad front could have already set in at this time. A purely southern immigration—from the eastern Baltic region across the present-day Gulf of Finland—could have had a role only during the latter part of the Yoldia period, since southern Finland was earlier almost completely under water.

Much as in Sweden, subfossil remains of a pronounced alpine flora and fauna have been found only in the extreme south, in the Isthmus of Karelia and in the adjacent parts of Russia (Har. Lindberg, 1916, p. 3; Hyyppä, 1933, pp. 10 ff.), including the carabid *Pterostichus vermiculosus* (p. 672), which is now distributed westward only as far as Pechora. It must be assumed—as for Sweden (p. 710)—that in Finland the real alpine-subalpine organisms did not reach the fjelds from the south (southeast). Cajander's surmise (1921, p. 5) that this would have been possible along the supra-aquatic Maanselkä has remained unconfirmed. Even in northern Finland the inland ice has apparently been draining directly into the sea or into reservoirs (Sauramo, 1942, pp. 227, 228), so a terrestrial *Regio alpina* could scarcely come into existence in the immediate vicinity of the ice.

The various immigration routes from the south and the east to Finland (and the rest of eastern Fennoscandia)**—with the exception of the northernmost one—are not sharply separated from one another. However, the following may be appropriately left out of consideration:

1. From the south across the Gulf of Finland.
2. From the southeast across the Isthmus of Karelia, between lakes Ladoga and Onega, or between the latter and the White Sea.

*Salpausselkä" is a Finnish word which means "end moraine," but is more correctly described as a "recessional moraine"—General Editor.

**Åland and the rest of the southwestern Finnish Skärgård are left out here, since a separate section (pp. 236 ff.) has been devoted to them.

3. From the east, especially through Kuusamo and Salla.

4. From the northeast through Kanin to the Kola Peninsula.

719 1. The "*Baltic immigrants*" (Krogerus, 1925c) play an important role in southwestern Finland, which was first shown by Eklund (1931, pp. 88 ff.) with respect to the flora. The importance of this phenomenon for the coleopteran fauna has been elucidated by Palmén (1944 pp. 206 ff.). Postglacially the altitudinal conditions in the region of the Gulf of Finland have never been more favorable than today. The large size of the Baltic immigration group is to be ascribed primarily to the unusually favorable situation for *anemohydrochorous dispersal* in the estuarine region of the Gulf (Palmén, 1944), as discussed above (p. 604), where a list of the clearest examples among the carabids is provided. This immigration route is therefore utilized predominantly by *winged* insects. However, two constantly flightless species of *Carabus* (*C. cancellatus*) and *C. convexus*; p. 603) could have arrived hydrochorously from the same direction.

The important question arises as to how far immigration from the eastern Baltic region—directly or via southwestern Finland (including Åland and the remaining skärgård)—has affected Sweden as well. With regard to the Baltic islands, especially Gotland and the neighboring small islands (Sandön, Fårön), this question has been dealt with in detail (pp. 282, 287, 291) and the great importance of this migration route for winged forms emphasized. For two functionally brachypterous species (*Carabus clathratus, Cymindis macularis*) hydrochorous transport from the same direction was assumed.

Palm (1942, pp. 49 ff.) investigated the possibility of eastern immigration across the sea directly to the mainland of central Sweden. He gives a list of 27 species of the fauna of the lower Dalälv River region (Upl, Gst, Dlr) which in Sweden have a more or less pronounced eastern distribution but seem to lack an area connection to the south (and the north). All of the species considered are winged, and Palm may have been correct in assuming anemochorous immigration from the east for a majority of them.

There are only a few carabids with a completely isolated area in east-central Sweden. The best examples are:

Agonum longiventre	*Demetrias imperialis*
Bembidion humerale	*Dichirotrichus rufithorax*
B. transparens	*Oodes gracilis.*

720 Some of these species have been considered earlier. *Dischirotrichus rufithorax* was said to have probably arrived synanthropously from the east (p. 633). The central Swedish stock of the dimorphic *Bembidion transparens* may have immigrated anemo-(hydro-)chorously in the macropterous form (p. 395). Nothing can be said about the immigration route of the two almost identically distributed species, *Demetrias imperialis* and *Oodes gracilis*, since their Swedish area is equally isolated to all sides. They were considered as warm period relicts and represent only the extremes of a whole series of species that have

found a favorable refuge in the central Swedish warm region (p. 691).

Possibly the same interpretation may be applied to *Agonum longiventre* (Palm, 1942, p. 55). But this is doubtful for three reasons. First, the Swedish record locality of the species—at any rate macroclimatically considered—is not a pronounced warm region. Second, the curculionid *Larinus sturnus* Schall. in Sweden has a nearly identical area, and this species is distributed in Finland so far north (as far as Oa, Sb, Kb; *Catalogus*, 1939, p. 107) that it cannot have any definite heat requirement. Third, *Agonum longiventre* actually has its nearest connection with the east. The species is of course missing from Finland, but was found in Estonia near Narva and also in the Leningrad region. In Central Europe it is likewise markedly eastern (Horion, 1941, p. 327), and it is therefore difficult to suppose that the Swedish area represents the result of a southern immigration. But it must be conceded that the last-mentioned objection is also partly applicable to *Oodes gracilis*, which at any rate in Germany is markedly eastern (map in Lindroth, 1943a, p. 119). In the case of this species it is wise to leave the immigration route unresolved, but in the case of *Agonum longiventre* we are justified in assuming an eastern immigration to Sweden by the aerial route. The present-day restriction to a very small area may be explained (p. 696) by the "virgin forest character" of the region.

It seems unambiguous that the two central Swedish records of *Bembidion humerale* are the result of migration from Finland, where this very active flier has a much wider distribution. It is possible that this is also true of *Pterostichus angustatus*.

It is more difficult to decide whether flightless insects, too, could have reached Sweden from the eastern Baltic region or Finland without the help of
721 human displacement. *Crepidodera nigritula* Gyll. ought to be considered which Palmén (1944, p. 228) includes among the "Baltic" immigrants. In Sweden this species occurs only in Sdm and Upl (it is also missing from Denmark) and seems to be constantly brachypterous. However, in Finnish drift material (Palmén, 1944, p. 57, and *in litt.*), 4 macropterous specimens were found. It is thus conceivable that the species originally reached Sweden in the macropterous form—as was surmised hypothetically for *Bembidion transparens* (p. 395). On the other hand, as discussed above (p. 287) the dimorphic *Cymindis macularis* may actually have colonized the small island of Sandön in the outer skärgård of Stockholm by hydrochorous transport in the brachypterous form.

2. The "*Karelian*" immigration route between the Gulf of Finland and the White Sea, represents so to speak the normal direction of immigration of the Finnish flora and fauna. However, it was fully opened only at the end of the Ancylus period, since the northern part of the Isthmus of Karelia and present-day coastal regions of Finland were earlier submerged (Fig. 99; see also map in Sauramo, 1942, p. 228). This situation has certainly substantially contributed to the fact that the late-glacial "Dryas flora" of the extreme southeast of Finland (Hyyppä, 1933, pp. 10 ff.), as far as is known, has not advanced farther north.

The forest seems to have reached into southeastern Finland as early as the "Salpausselkä" stage (Hyyppä, 1933).

The "Karelian" immigration group of flora has been most recently treated by A. Kalela (1943, pp. 37 ff.), that of the coleopteran fauna by Palmén and Platonoff (1943, pp. 171 ff.).

An enumeration of individual cases of more or less distinct "Karelian" immigrants has little purpose, since this characteristic is usually evident from the relevant distribution map. On the other hand the same two questions can be raised here that we attempted to answer above with respect to the southern immigration element in Scandinavia, namely:

a. Did the pronounced alpine and subalpine species of the present-day fauna of Finland also arrive from the southeast?

b. How far north and west has the "Karelian" immigration group advanced?

a. The first question has been answered above on the basis of botanical evidence. The late-glacial, pronounced alpine flora and fauna that demon-
722 strably occurred in the Isthmus of Karelia (among the carabids *Pterostichus vermiculosus* Mén.) were apparently not in a position to follow the retreating ice edge north. Valle (1933, p. 103) is of the same opinion with respect to the immigration of pronounced alpine Lepidoptera.

b. Early on the possibility of immigration to Finland was already available to the "Karelian" species. The significance of this fact for the flora has been considered in detail by Hiitonen (1946). Although at first—before the Ancylus period—the land largely lay under water and was fragmented into an enormous skärgård, these species had "plenty of time" to colonize a wide region. The southern Swedish group (which arrived through Skåne) only later reached comparable latitudes in Scandinavia. Where these two stocks have not merged and lost the imprint of a double provenance, the Finnish stock has almost without exception advanced farther north. In some cases this difference is due to climate (p. 459), in others due to the history of immigration. But it is just the most pronounced examples of the last-mentioned type that are not—or not exclusively—of "Karelian" origin in the sense used here by Palmén and Platonoff (1943, pp. 167 ff.). Another, more northern element is also involved. It is therefore appropriate to postpone further consideration (see p. 724).

Let us first take up another question: To what extent are these species with both "Baltic" and "Karelian" immigration? And is the double origin always evident in such cases? This theme has already been considered with respect to Coleoptera as well (Palmén and Platonoff, 1943, p. 183; Palmén, 1944, pp. 217, 227). All of the five examples cited show a more or less pronounced gap halfway along the south coast of Finland. Four of them (*Aphodius lividus* Ol., *Aphthona euphorbiae* Schrk., *Crepidodera nigritula* Gyll., *Heterocerus marginatus* Fbr.) are in addition represented in the drift material of the Tvärminne region (Nl), but not the fifth species, *Bembidion monticola*. In this

case it appears to me somewhat bold to assume a "Baltic" immigration, since all northern limiting localities of *Bembidion monticola*, as far as I can decide, have a relict character (see map by Netolitzky and Sainte-Claire Deville, 1914). *Pterostichus aethiops* may occupy a similar position.

723 A distribution gap halfway along the Finnish south coast need not be due to the history of immigration. There are, namely, two other facts to be considered: First, the coastal stretch Helsinki-Viborg (or at any rate Pärnå-Viborg) has been entomologically less explored than the two "corners" of the country. Second, we cannot rule out a climatically determined gap in that region; a lacuna here is also shown by *Quercus* (Fig. 61, p. 437). Carabids that show a more or less distinct gap on the Finnish south coast are (omitting those found only in drift material in the southwest):

	o	*Acupalpus dorsalis*	o	*B. transparens*
	w?	*A. exiguus*	o	*B. unicolor*
	w?	*A. meridianus*	o	*Bradycellus collaris*
	o	*Agonum assimile*	w?	*B. similis*
	o	*A. dolens*	k	*Calathus ambiguus*
	o	*A. ericeti*	k	*C. fuscipes*
	o?	*A. livens*	w	*Carabus cancellatus*
	k	*A. marginatum*	k?	*C. convexus*
	w?	*A. micans*	w?	*C. violaceus*
	k	*A. ruficorne*		*Cicindela maritima*[1]
	o	*A. thoreyi*	o	*Cychrus caraboides*
	o	*Amara apricaria*	o	*Cymindis macularis*
	o	*A. communis*	o	*Dichirotrichus rufithorax*
	o	*A. consularis*	o	*Dyschirius lüdersi*
	o	*A. famelica*		*D. obscurus*[1]
	o	*A. familiaris*	o	*D. politus*
	o	*A. ingenua*	o	*Harpalus fuliginosus*
	o	*A. montivaga*	k?	*H. rubripes*
	o	*A. municipalis*	o	*H. tardus*
	o	*A. ovata*	k?	*Lebia cyanocephala*
	?	*A. quenseli*	k?	*Metabletus foveatus*
	k	*A. spreta*	w?	*Microlestes minutulus*
	?	*Asaphidion pallipes*	?	*Nebria gyllenhali*
	o	*Badister bipustulatus*	o	*Notiophilus germinyi*
	o	*B. dilatatus*	w?	*N. pusillus*
	w	*Bembidion biguttatum*	k	*Odacantha melanura*
	?	*B. grapei*	w?	*Olisthopus rotundatus*
	o	*B. properans*	o	*Panagaeus crux-major*
724	w	*Bembidion schüppeli*	o?	*Pterostichus angustatus*

[1]Not found in quicksand regions (Krogerous, 1932, p. 26).

w.	*P. aterrimus*	o?	*Trechus discus*
k?	*P. gracilis*	o?	*T. micros*
o	*Tachys bisulcatus*	o	*T. rivularis*

The code indicates the assumed cause of the gap; k—climatic, w—history of immigration, o—due to insufficient exploration, ?—unknown factors.

The long list shows how common a distribution gap is along the Finnish south coast, but at the same time that more than one-half of the cases (35 of 64) are very probably attributable to insufficient entomological exploration. Hence great caution must be exercised in proposing a "double" immigration for southern Finland. On the other hand it is obvious that in most species with such a "double" immigration the two stocks soon lost their respective provenance by a merging of the geographical characteristics. So I will not discount the "Baltic" immigration, but merely point out that it is not possible to confirm it in every case.

3. It has already been established that an immigration of plants and animals took place across the eastern border of Finland in the region of the Arctic Circle. Cajander (1921, p. 9) has described how he visualizes the migration of *Dianthus superbus* through Kuusamo to the Gulf of Bothnia. Lists of plants with similar distribution and similar assumed history have been provided by Erlandsson (1939) and A. Kalela (1943, p. 50). A good zoogeographical account—including the history of immigration—of the insect fauna of the Paanajärvi lake region is given by Platonoff (1943, pp. 108 ff.) on the basis of Coleoptera. Krogerus (1932, p. 252) had earlier proposed the Kuusamo route for the immigration of some quicksand insects, including *Cicindela maritima* and *Dyschirius obscurus*.

Among carabids there is in fact an imposing series of species which, judging from the usual distribution map alone, are to be interpreted as eastern immigrants both above and below the Arctic Circle. Examples (br = functionally brachypterous):

		(*Agonum micans*)	?	(*Bradycellus ponderosus*)
	br	(*Bembidion aeneum*)		(*Cicindela maritima*)
		B. hasti	br	*Dromius sigma*
725		*B. litorale*		*Dyschirius lüdersi*
		(*B. ruficolle*)		(*D. obscurus*)
		B. saxatile		(*D. septentrionum*)
	br	*B. schüppeli*		*D. thoracicus*
		B. tinctum		*Harpalus fuliginosus.*
	br	*B. transparens*		

The species in parentheses are unknown along the shore of the White Sea, which is unimportant, given the poor exploration of this region. Three species (*Bembidion hasti, B. transparens, Dyschirius obscurus*) are strikingly isolated along the Gulf of Bothnia.

Even a superficial scrutiny of the list gives a strong impression of the ecological homogeneity of the species concerned. With the exception of two species (*Bradycellus, Harpalus*; and less regularly *Dromius sigma*), all of them, 14 of 17! species, are markedly ripicolous. The corresponding group of plants ("*Primula sibirica* group"; Erlandsson, 1939) distinctly shows the same characteristic. Of the 20 species mentioned there is only one (*Moehringia lateriflora*) that does not grow more or less regularly along the shore—where most of them are found exclusively.

It is quite natural that attempts were made to explain this animal and plant group by an earlier aquatic connection between the White Sea and the northern end of the Gulf of Bothnia. Kuusamo and the eastern and southern parts of the parish of Salla (Kuolajärvi lake) are situated east of the main watershed toward the White Sea (see map, Fig. 45, p. 391). This is geomorphologically a poorly marked area between the Oulankajoki (including its tributaries), emptying into the Paanajärvi, and the water system of the Kemijoki. It is just the valleys of the Paanajärvi and the Kutsajoki in southern Salla that have been considered as "doors" for eastern flora and fauna (A. Kalela, 1943, p. 50).

An idea of the current thinking of Finnish geologists (Hyyppä, Sauramo) concerning the distribution of land and water in the northeastern Finland in the oldest postglacial period (*s.l.*), is given in the maps, Figs. 104 and 105. Noteworthy are first the remarkably early melting of inland ice in these regions, second the low elevation of the land, which in part was responsible for a great extension of the White Sea westward and in part caused the extensive inundation of parts of Finland closest to the ice edge.

726 Erlandsson (l.c.) states the watershed in the Kuusamo-Salla region was breached by two straits (especially in the Baltic Ice Lake period!) and refers to Hyyppä. However, in his contribution of 1936 (pp. 437 ff.), he speaks only of "discharge channels," and even during the Yoldia period in this region there was apparently no open connection with the White Sea (Fig. 105). The distance between the western bays of the White Sea and the offshoots of the Baltic Ice Lake or of the Yoldia Sea in Kuusamo-Salla was less than 10 km (in the
727 Kutsa River region) or 2–3 miles (west of Paanajärvi), respectively. Especially in the earlier period, when these passes were occupied by enormous rivers, they may have offered excellent "migration routes" for ripicolous (and other) animals and plants coming from the east. Keeping *Bembidion aeneum* in view, for which species we have assumed a slight halobionty (p. 521), it is important that from time to time Paanjärvi was a western offshoot of the White Sea and
728 so passed through a saltwater stage. The two specimens of the species found here were both brachypterous (Fig. 49, p. 400), and we are therefore justified in assuming that the species had already immigrated in this early period.

Such an assumption is not at all improbable. The studies on pollen analysis by Hyyppä (also 1941, p. 609) have, as it seems, unambiguously shown that

the climate during the latter part of the Baltic Ice Lake period in the eastern border regions of northern Finland was already so favorable that the ice-free and supra-aquatic parts on both sides of the present-day border of the state were covered with *Pinus-Betula* forests. When the distribution of land and water was favorable (Baltic Ice Lake period and Yoldia period) for an eastern immigration this could have been undertaken by other than purely alpine-subalpine species as well.

726 Fig. 104. Final stage of the Baltic Ice Lake. According to Sauramo (1942). Cf. Fig. 97 (p. 699).

The question must be asked whether the group that immigrated through Kuusamo-Salla is to be considered simply as the "vanguard," as the forward patrol of the "Karelian" invasion or whether a separate origin—completely or partly—should be ascribed to it. A. Kalela (1943, pp. 46, 49) favors a sort of compromise. He thinks the plant group that arrived in the region of the Finnish state through Kuusamo-Salla belongs partly to the "Karelian" element, partly to a more northern element, which has spread from the east along the south coast of the Kola Peninsula.

Had the wing-dimorphic species not provided a good clue, I could not have ventured an opinion on this issue. However, the dimorphic maps of a number of species, which were considered above from this viewpoint too, bring us a step closer to an explanation:

Bembidion guttula (p. 387, Fig. 42)
B. nigricorne (p. 389, Fig. 44)
B. transparens (p. 389, Fig. 45)
Carabus clathratus (p. 381, Fig. 38)
Pterostichus lepidus (p. 381, Fig. 37)
P. minor (p. 387, Fig. 43)
P. strenuus (p. 395, Fig. 47).

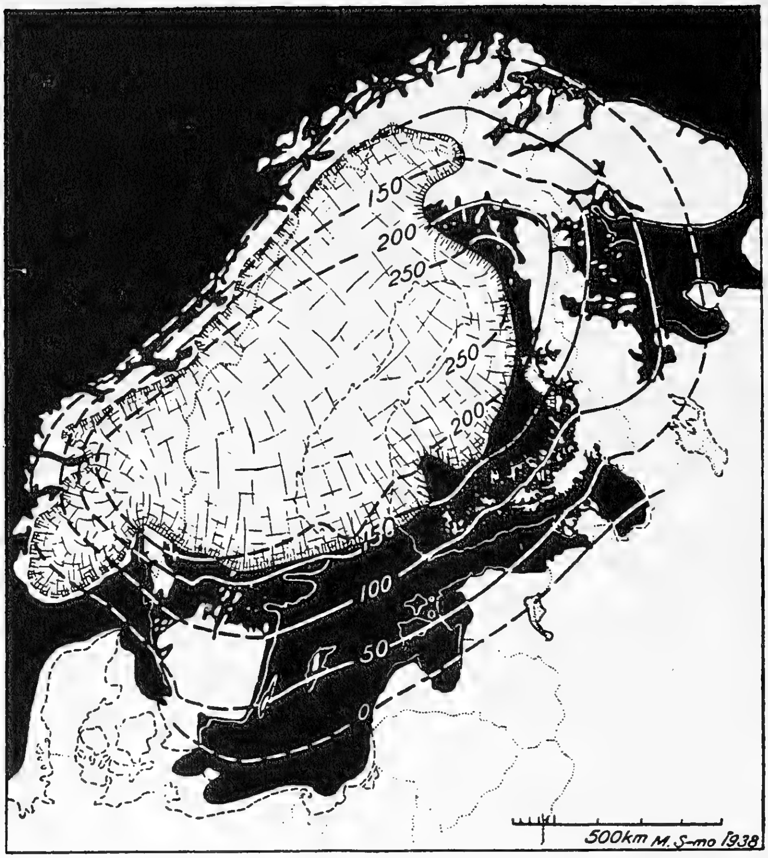
The distribution of macropterous and brachypterous individuals of these species in eastern Fennoscandia against all expectations shows an increase in the component of flightless individuals in the north. From this it may be
729 concluded that the immigration via Kuusamo-Salla (of *Bembidion nigricorne*, possibly also of *Carabus clathratus*, somewhat more southerly) was functionally separated from the normal southeastern "Karelian" immigration route.

Is it conceivable, as A. Kalela assumed in respect of several members of the "woodland flora," that the carabids in question spread from Kanin-Mezen along the south coast of the Kola Peninsula?

Of the 24 "Kuusamo-Salla species" in the two lists, 15 species are not found along the south coast of the Kola Peninsula (however, *Pterostichus lepidus* has been found near Lm Kantalaks). It must be noted that, thanks to the intensive research by Finnish entomologists of the last century, the southern coastal regions of the Kola Peninsula are among the coleopterologically best-known parts of northern Fennoscandia.

Of the same 24 species, 20 are unknown from Kanin-Mezen east of the White Sea (only the following are present: *Bembidion hasti, B. saxatile, B. transparens, Dyschirius septentrionum*). This cannot be considered as conclusive, although Poppius (1909a) collected energetically on the Kanin Peninsula. Of these 20 species, as far as is known, 11 or 12 are also missing from the Pechora region. Of these latter, 2 of course occur south of the White Sea (in the Archangel region) but without any contact with the stock considered here.

Of the same 24 species, as far as is known, 7 species are totally missing from northern European Russia: *Bembidion aeneum, B. nigricorne, B. ruficolle,*



727 Fig. 105. Initial stage of the Yoldia Sea. According to Sauramo (1942) (with corrections by that author, *in litt.*, in respect of position of eastern ice edge). Cf. Fig. 98 (p. 700).

Bradycellus ponderosus, Cicindela maritima, Harpalus fuliginosus, Pterostichus minor. Dyschirius lüdersi and *D. obscurus* are doubtful.

These considerations led me to no other conclusion than that most species of the "Kuusamo-Salla group" are functionally (in their history of immigration) separated not only from the normal, southeastern "Karelian" group but also from the "Kanin-Kola group." Caught in the cross-fire as it were, the element under consideration must have, considered geographically, an intermediate origin, somewhere around the White Sea. One is led to the conclusion that somewhere on the western half of the White Sea a Würm refuge existed, which was isolated both to the south (by ice) and to the east (by water). If

during the maximum of the last glaciation the seashore—as seems probable (p. 772)—was here considerably lower than today, this assumption is not so
730 implausible as may appear from the map today or, in particular, from a map of the late-glacial and early postglacial period (Figs. 104, 105). Moreover, if the peculiar occurrence of *Bembidion chaudoiri* on the White Sea is actually as isolated as we at present assume, this would provide further support for the above view. A conclusive answer can be given only after thorough exploration of the fauna along the western and southern shores of the White Sea, which certainly will take time. It may also be mentioned that botanical indices favor a Würm refuge here, possibly in the Hibinä region (Nordhagen, 1935, p. 132).

It is possible that the separation between the "Kuusamo-Salla group" and the "true Karelian" group was enhanced from time to time by an aquatic connection between the White Sea and the Gulf of Finland (via Onega-Ladoga). Hyyppä (1944, pp. 122 ff.; also Platonoff, 1943, pp. 112–113, footnote) thinks such a connection is indispensable, but it is not generally accepted by others (Tanner, 1930, p. 384; but see also Astrid Cleva-Euler, 1934, p. 92). Poppius' idea (1909b, pp. 60–61) that some aquatic and riparian species (Coleoptera, Hemiptera) utilized this aquatic route during a dispersal from the Gulf of Finland into the White Sea region is certainly mistaken.

4. The possibility of immigration of plants across the estuarine strait of the White Sea from Kanin-Mezen to Kola has been considered by A. Kalela (1943, pp. 41, 47). He attaches great importance to this route, both for true alpine species (tundra plants) and for woodland flora. He cites Ramsay and Auer, according to whom during the late-glacial period this strait was considerably narrower (see also Tanner, 1930, p. 388), or there was (according to Auer) even a firm land connection between Kola and Kanin. Astrid Cleve-Euler (1934, p. 99) and Har. Lindberg (1938, p. 27) also speak of a fresh-water stage of the White Sea (cf. on the other hand, Tanner, 1930, p. 385). The isolated, certainly old occurrence of *Dichirotrichus pubescens* in the south on the White Sea seems to show that the salt content in the postglacial period was never below 6 per mille. The possibility of a separate immigration of Coleoptera to the Kola Peninsula has been considered by Palmén and Platonoff (1943, p. 185).

731 The Carabidae that suggest such an immigration route are naturally in the first place those, restricted in Fennoscandia to the Kola Peninsula (br—brachypterous):

**	*Agonum aldanicum*	**	br	*Diachila polita*
	Amara peregrina	*	br	*Pterostichus fastidiosus*
**	*Bembidion crenulatum*	**	br	*P. middendorffi*
	B. repandum	**	br	*Trichocellus mannerheimi.*

The species marked with one asterisk (*) is found in the Ponoj region (province of Lj) in the extreme east; those marked with two asterisks (**) occur

exclusively in this region. At least the last four species are true tundra animals, although they also occur the farthest east in the northern parts of the Taiga.

Just these 4 tundra species are wingless and support the assumption that a firm Kola-Kanin land connection in the Ponoj region has existed (A. Kalela, 1943, p. 41). It is namely difficult to see how they could have tolerated hydrochorous transport in the highly saline water of the estuarine strait of the White Sea (p. 517). Overland immigration via a southern detour around the White Sea seems quite improbable in view of the present-day distribution of the 4 species.

Half of the 8 species are known from Kanin (*Agonum aldanicum, Bembidion repandum, Diachila polita, Pterostichus fastidiosus*), a much larger proportion than of the "Kuusamo-Salla species" above. But historically *Bembidion repandum* and *Agonum archangelicum* (which is distributed farther south along the White Sea coast), both of which are absent from the eastern part of the Kola Peninsula, may belong to the latter group.

The distribution of the (7–) 8 "Kanin-Kola species," restricted mostly to the extreme eastern part of the Kola Peninsula, need not be taken to signify a late (possibly continuing) immigration. It is probable that these continental species have reached their existence limit here in the face of a more oceanic climate.

Palmén has rightly emphasized (Palmén and Platonoff, 1934, p. 169; Palmén, 1944, p. 208) that a fixed geographical terminology in respect of the different immigration groups is better than naming them according to the compass bearings, chiefly because the latter is valid only for restricted
732 regions. If one wishes to name the four—from the general Fennoscandian viewpoint—eastern-immigration groups of the fauna (and flora) of Finland, according to this "fixed" terminology the following names may be proposed:

1. Baltic group.
2. Karelian (possibly southern Karelian) group.
3. White Sea group.
4. Kanin-Kola group.

It only remains to investigate how far the species (or stocks) that immigrated across Finland—whatever the route—have reached south and west in Scandinavia. In respect of Coleoptera this question has been considered chiefly by Lindroth and Palm (1934, pp. 120 ff.), Palm and Lindroth (1936, pp. 32 ff.), and Palmén and Platonoff (1943, pp. 171 ff.). These authors are unanimous in that *the northeastern group is of decisive importance for the colonization of northern Scandinavia, and that some members thereof have even reached the southernmost parts of Norway and Sweden.*

Opinions may differ on whether the above-mentioned examples are always correct. For instance, I must presume that *Gnypeta coerulea* C.R. Sahlb., extending as far as southernmost Norway, considered as extreme by Palmén and Platonoff (1943, p. 176), partially survived the Würm glaciation in Scandi-

navia. It is a boreo-British species (Lindroth, 1935a, p. 599), which has at any rate succeeded in doing this in the British Isles. A similar reservation applies to *Phytobius velaris* Gyll. (Lindroth and Palm, 1934, p. 122). The occurrence on Små, if it can be confirmed, might be considered as a relict of a southern immigration. The "Karelian" stock seems to have touched only southern Finland, and the main Scandinavian range is most probably that of an interglacial relict. A precise mapping of this species would be very rewarding.

However, it cannot be denied that some northeastern immigrants to Scandinavia reached very far south, and I will try to give some clear instances. It should be expected of them first that they have (as far as is known) uninterrupted distribution into regions east of the former Würm ice, second that they are missing from northwestern (or in general from) Central Europe, and third that they are absent from the assumed western and northern Fennoscandian Würm refuges or occur there only in isolated outposts.

733 Naturally in Scandinavia there are not many widely distributed species that meet all these conditions. The clearest examples are:

Bembidion tinctum (Fig. 118, Supplement), in Sweden south to Mdp, and especially *Tachyta nana*, which in the south has even reached northern Skå. It is missing from Denmark and northwestern Germany (Horion, 1941, p. 171). *Agonum mannerheimi*, with the peculiar relict occurrence near 12 Vardal, and *Tachys bisulcatus* (up to Skå) also seem to be eastern immigrants.

I must confess I have my doubts about this thesis in the case of species like *Notiophilus reitteri* and *Pterostichus adstrictus*, which were earlier (Palm and Lindroth, 1936, p. 34) assumed to be postglacial northeastern immigrants. Both occur within the limits of the assumed Norwegian Würm refuges. The dimorphic *Notiophilus* seems to be everywhere functionally brachypterous with a relatively poor capability of dispersal†.

Even *Amara erratica* and *A. torrida*, which have been repeatedly cited (for instance, Lindroth, 1939a, p. 246; Holdhaus and Lindroth, 1939, p. 261) as typical examples of a northeastern postglacial immigration to Scandinavia could have had a more complicated origin. Of course their almost identical Scandinavian southern limits are undoubtedly dynamical and not dependent on existence factors (Holdhaus and Lindroth, l.c.). However, especially in the case of *A. torrida* there seems to be nothing short of a concentration at the assumed northern refuges, which cannot be ascribed to erratic exploration alone. It is possible that today's seemingly homogeneous area is the result of merging of interglacial and northeastern postglacial stock. On this assumption one might be inclined to argue that "sufficient time" was available for dispersal farther south along the Scandinavian chain of fjelds. But with this we are touching on the obscure problem of the *speed of dispersal*, which varies quite inexplicably in different species—and at different times in the same species.

†(cf. p. 823; suppl. scient. edit.)

Peculiar instances were provided in the earlier section on the recent faunal changes in our region (pp. 621 ff.).

The (partially) northeastern origin is especially evident in those Scandinavian species that have two stocks in the environs of the Bothnian Sea, a south-Scandinavian and an east-Scandinavian, which have still *not* met. This is
734 the phenomenon of "double" immigration (Lindroth and Palm, 1934, p. 124).

As discussed above (p. 714), in the case of double immigration in the Bothnian coastland, the Finnish stock has normally reached farther north than the Swedish stock. In several cases it has even encroached into the region of the Swedish state, where sooner or later a merger with the western stock will follow or has already taken place.

If the gap on the Swedish side still exists, the double origin appears readily evident. However, as a precaution it must be remembered that according to the July map (Fig. 63, p. 452) very low summer temperatures are recorded in the border regions Ång-Vbt, where there seems to be a true gap (for instance, in the case of *Dyschirius thoracicus, Notiophilus palustris*) or at least a thinning out of record localities (for instances in the case of *Agonum piceum* and *A. versutum*, with reservations on account of insufficient exploration). It seems conceivable that this minus region was strengthened during the subatlantic climatic deterioration and thus divided an originally homogeneous area in the Bothnian coastland into two parts. In respect of one of the species listed below (*Pterostichus niger*) the subfossil record near Dlr Evertsberg from the sub-boreal-atlantic borderline period (p. 674) seems to show that it was once more widely distributed. The reservation about the significance of the "Bothnian gap" mentioned here, in respect of the history of immigration, nevertheless seems to be largely of theoretical interest. The gap in almost every case has a different (mostly more northerly) position and in my opinion is never climatically determined.

In the following list there are also some dimorphic species with no "Bothnian gap," but in which the limit between the two stocks was determined well enough from the distribution of macropterous individuals.

Instances of species with double immigration into the Bothnian coastland, in which the eastern stock has advanced farthest—on Swedish region—are:

Agonum dolens
735 *A. piceum*
A. thoreyi (Fig. 95, p. 675)
Bembidion guttula (Fig. 42, p. 386)
Carabus clathratus (Fig. 38, p. 380)
Cymindis macularis
Dromius sigma
Dyschirius obscurus
D. thoracicus
Notiophilus palustris
Panagaeus crux-major
Pterostichus coerulescens
P. lepidus (Fig. 37, p. 379)
P. minor (Fig. 43, p. 388)
Pterostichus niger
P. strenuus (Fig. 47, p. 396)
P. vernalis (Fig. 36, p. 378).

An extreme instance among other Coleoptera is provided by *Paratinus femoralis* Er., which was known in Finland northward as far as Ob, in Sweden only on Skå. But I discovered it in 1939 on the island of Sandön in the skärgård of Nbt Luleå.

Finally it may be noted that the eastern postglacial immigrants through Finland, in some cases reached Sweden also by direct immigration across the sea, partly through Åland (p. 719) and partly across the Bothnian Sea, especially at its narrowest part, Kvarken (pp. 381, 593).

The peculiar species *Amara majuscula* (p. 622) has colonized southeastern Fennoscandia on a broad front through the air.

III. THE PROBLEM OF "WÜRM HIBERNATION"

When Nathorst (1871) made his famous discovery of the subfossil *Dryas* and other alpine plants near Alnarp on Skåne, it provided the first palpable proof that the Scandinavian fjeld flora was pushed into more southern regions during the Ice Age. Of course the account of the Scandinavian faunal history by Sven Nilsson (1847) anticipated this viewpoint. Gradually the geologists established signs of Quaternary land ice in all parts of Fennoscandia. It was logical to think that the ice in this part of Europe had destroyed all life, and that the present-day Fennoscandian flora and fauna as a whole immigrated in the postglacial period from surrounding land which had remained ice-free. Sernander called this long-held view the *tabula rasa* theory.

It was an important finding for a correct understanding of the biological effect of the Glacial Epoch that the so-called Ice Age was a complex of several separate glaciations, each of which, geologically as well as biologically, presented a separate problem. A systematic arrangement of the glacial for-
736 mations during different glacial periods was first undertaken for the Alps (Penck and Brückner, 1901–1909), where at least four glaciations were established. In Fennoscandia their traces could not be consistently separated from one another for understandable reasons; however, since the southern marginal deposits of the northern inland ice in northern Germany were attributed to three or four separate glaciations (Richter, 1937) it was generally assumed by geologists that Fennoscandia had gone through at least three Quaternary glaciations, with long intervening climatically favorable periods (for instance, A. Wagner, 1940, pp. 141 ff.). The estimated durations of the different glaciations varied widely according to the different methods of calculation. At any rate they, as well as the interglacial periods, lasted much longer than the entire postglacial period (hence > 20,000 years long).

The ice cover was most extensive (at any rate in Europe) during the penultimate glaciation, generally called the *Riss* (Fig. 101, p. 705). The subsequent, last interglacial period is known partially also from Swedish deposits (p. 673) and indicates a climate which from time to time was as favorable as today's.

During the *last* glaciation (Würm) the northern inland ice was less extensive in all directions (Fig. 102, p. 706). Among other places, the southwestern part of Jutland lay beyond the ice edge. Since a climatically ameliorative influence on the part of the sea, the Gulf Stream included, can be assumed for the whole of Western Europe, the idea developed early that even on the Scandinavian west coast, ice-free regions would have existed throughout the Würm Ice Age.

At first this problem was purely biogeographical. Blytt (1893, p. 26) tried to explain the occurrence and distribution of some Norwegian fjeld plants on the assumption of Ice Age refuges; he was followed by Sernander (1896, p. 117). On a larger scale, still on the basis of botanical material, the question was considered by A.M. Hansen (1904, pp. 282 ff.), who visualized the "hibernation" of at least 300 phanerogams in Norway—and indeed along the west coast, but not on nunataks.† Wille (1905) assumed a refuge in the environs of 8 Nordfjord.

In 1913, two important phytogeographical contributions (Th. Fries, Teng-
737 wall) posited a Würm hibernation in Norway for many fjeld plants. Fries (p. 314) believed the refuges were chiefly ice-free coastal stretches; Tengwall (p. 269, in respect of southern Norway) visualized them as isolated nunataks. These two studies carried more conviction than the earlier ones, especially because they drew on actual geological material. Since shortly before, Vogt (1912, pp. 6, 47) and Enquist (1913, at greater length in 1918, for instance, pp. 5 ff.) had shown, that parts of the outermost Lofoten islands were located beyond the ice edge even at the Würm maximum (also according to Ahlmann, 1919, pp. 217, 238).

Nordhagen, in a series of resourceful contributions (1933, 1935, 1936), was still more successful in working with a combination of botanical and geological facts—the latter largely from his own observations. The prevailing view of the Nordic biogeographers on the Fennoscandian Würm refuges has been taken predominantly from his publications. Among other things, he has attempted a more precise localization of these refuges, which is depicted in the map in Fig. 106 (p. 739).

Other botanists who have effectively contributed toward a solution of the "hibernation question," and whose results are considered below, are: Smith (1920, pp. 138 ff); Elfstrand (1927); Degelius (1935, pp. 297 ff.); Nannfeldt (1935, 1947); Holmboe (1937); Faegri (1937, pp. 433 ff.); Björkman (1939, pp. 218 ff.); Arwidsson (1943, pp. 98 ff.); Dahl (1946); Lindquist (1948, pp. 319 ff.); Ahlner (1948, pp. 140 ff.).

The Nordic zoologists first hesitatingly followed in the footsteps of their botanical colleagues. The first of these was Stejneger (1907, 1908). In 1910 Sparre Schneider also clearly expressed the idea of interglacial relicts in the

†(= Rocks or mountains which project from glaciers and mass of inland-ice; suppl. scient. edit.).

northern Norwegian fauna. Wahlgren (1919) has used the "hibernation hypothesis" to explain the so-called western Arctic element of our lepidopteran fauna. Ekman (1920; 1922, pp. 397 ff.) considers the lemming (*Lemmus lemmus*) to be the only definite Würm hibernator of the Scandinavian fauna. In recent years it is chiefly the entomologists that have shown interest in these questions: in addition to Wahlgren, Brundin (1934, p. 174), Strand (1935, pp. 67 ff.; 1946, pp. 22 ff.) and myself (especially Lindroth, 1933, 1935a, 1935b, 1939a, 1941, 1948a; Holdhaus and Lindroth, 1939).

Among authors who have dealt with similar "hibernation problems" in other regions mention may be made of the following:

738 The Faeroes: Spärck (1924, p. 502), West (1930a, pp. 87 ff.).

Iceland: A.M. Hansen (1904, p. 351), Lindroth (1931, pp. 557 ff.)

Greenland: Gelting (1934, pp. 250 ff.), Böcher (1938, pp. 312 ff.).

Remaining Arctic islands: Wahlgren (1920), Strand (1942), Lynge (1934).

North America: Fernald (1925, 1929), Raup (1941).

The faunal history of the British Isles is discussed below (p. 793).

In the Central European mountains, chiefly in the Alps, these questions center on the so-called "massifs de refuge" (for instance, Heberdey, 1933).

Reinig (1937, for instance, Fig. 13, p. 50) attempted to trace back the entire faunal history of the Holarctic region to a series of Ice Age refuges.

Criticism of the hibernation theory was expressed by Tanner (1930) from the geological viewpoint and by Wynne-Edwards (1937, 1939) from the botanical viewpoint.

On the basis of the coleopteran fauna we shall now attempt to take up the problem of Würm hibernation simply by posing three fundamental questions:

I. How is it possible to decide whether a species of animal or plant is a Fennoscandian Würm hibernator?

II. Is it possible to locate the refuges on a purely biogeographical basis?

III. Did climatic conditions during the Würm Ice Age actually permit the presence of a more richer fauna and flora in the Fennoscandian refuges?

I. It will be best to take as the basis of our study a species whose characteristic as a Fennoscandian Würm hibernator is clearly evident, namely *Simplocaria metallica* Sturm (Fig. 106, cf. Lindroth, 1948a, p. 19).

On the basis of well-known recent and subfossil records, the history of this species during the late-glacial period can be reconstructed as follows: During the last interglacial period it was a frequent species in Scandinavia; it is the only beetle present in all four known Scandinavian subfossil samples contain-
740 ing insects. It was pushed south to Central Europe by the inland Würm ice; subfossils were found in abundance near Deuben in Saxony (Nathorst, 1894) in "diluvial clay" (but it is uncertain whether this is from the Würm period). In the final phase of the last glaciation, the species was initially able to follow the ice edge at least in the east; it was found in late-glacial Dryas deposits near Ik Kivennapa (Poppius, 1911). Even today this southeastern postglacial

stock leads a relict existence as an extreme rarity in southern Finland. The two remaining Fennoscandian subareas are located in the fjeld regions and are completely isolated. They originate from populations that survived the Würm glaciation on the coast in the west and north.

The reliability of this reconstruction, which may also find favor with critics of the hibernation hypothesis, of course depends largely on the availability of subfossils. In other species considered here these are either not available or not so complete. Hence the important question: Is it possible to posit Würm hibernation of a species of animal or plant without any fossil records? In the present case: Is *Simplocaria metallica*, even by the recent distribution alone, a definite Würm hibernator?

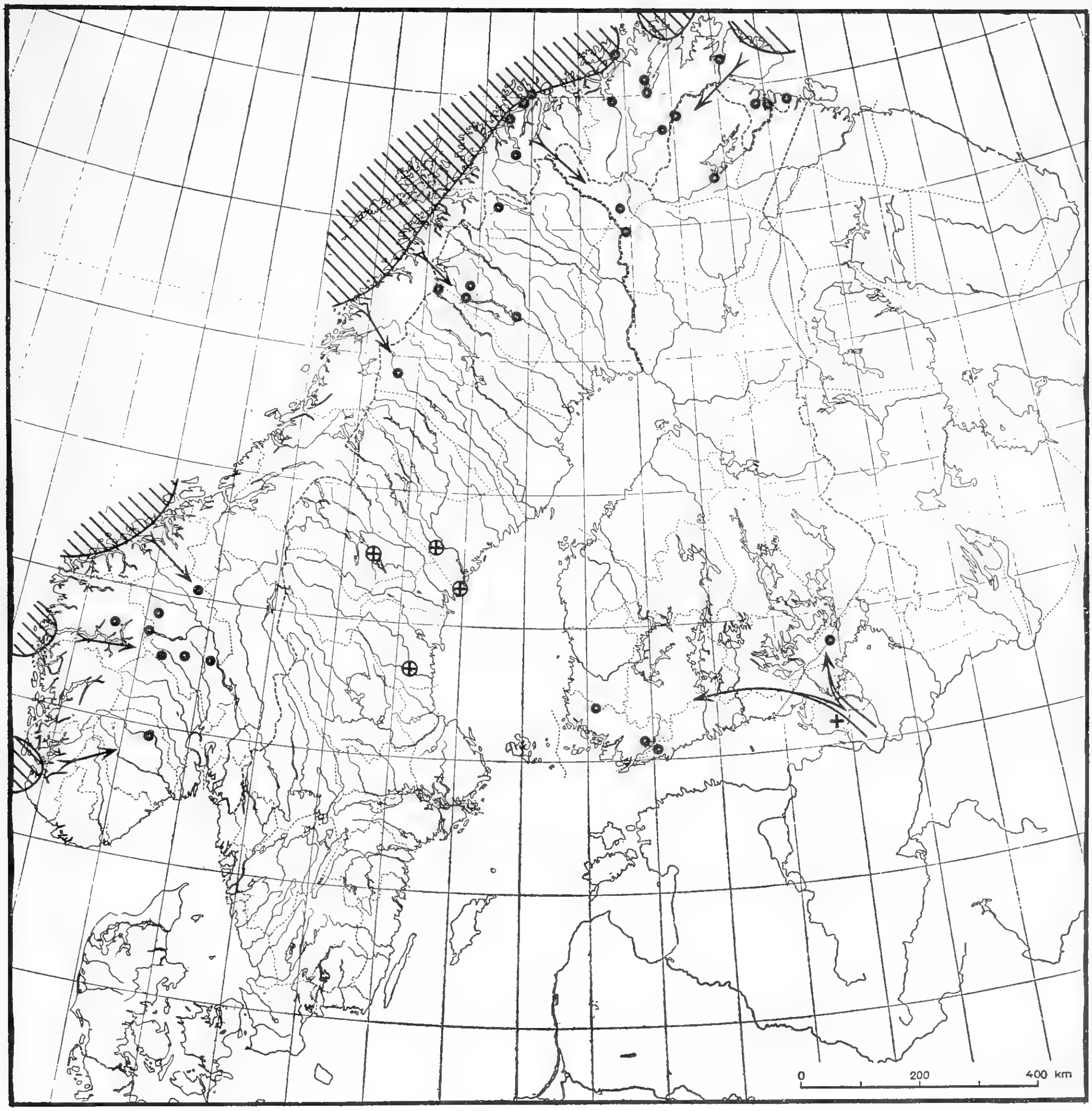
The last question must be answered in the affirmative, and hence the first, too. Let us here establish more precisely which characteristics of the present-day distribution picture of *Simplocaria metallica* support a Fennoscandian Würm hibernation (cf. also map in Plate XIII, Holdhaus and Lindroth, 1939).

a. The isolation of the Fennoscandian area (or of part of it). First and foremost, *Simplocaria metallica* lacks any connection to the east. The species is absent even from the Kola Peninsula and is altogether unknown east of Fennoscandia. Off the map (Fig. 106) there are localities only in the higher mountains of Central Europe (most northerly in Riesengebirge) and on Greenland. It is especially significant that this distribution makes a postglacial immigration from the east (from Russia and Siberia) impossible, since the in part well-explored Kola Peninsula also lies outside the area limit.

b. The occurrence of an isolated stock in a southern (climatically more favorable) locality, in the case of *Simplocaria metallica* the small isolated subarea
741 in southern Finland. This occurrence namely proves that the Fennoscandian main area was formed under the influence not of climatic factors but of the history of immigration of the species. The postglacial stock has not reached farther than southern Finland.

c. The bicentricity in the fjeld regions. Botanists tend to regard this as the most important circumstantial evidence for a glacial hibernation (further discussed below). In the case of *Simplocaria metallica* this viewpoint is especially relevant because—as a predominantly subalpine species—it cannot be bound to the higher montana regions and the far north on climatic grounds. The central Scandinavian gap is due to historical factors.

Not every Würm hibernator will show all of the three above-mentioned characteristics of *Simplocaria metallica*, since almost without exception one or more postglacial stocks have "adversely" affected the distribution pattern. Actually among the Fennoscandian carabids there is only one species (*Elaphrus lapponicus*) that forms a valid counterpart. Its area is completely isolated to the east, the remains of a postglacial stock are found in a relict locality in Latvia, and the bicentricity in Fennoscandia is clear. Here again the fossil records



739 Fig. 106. *Simplocaria metallica* Sturm. Assumed Würm refuges are hatched (according to Nordhagen, 1933, 1935).

(p. 699) show on the one hand that the species was native to Fennoscandia during the interglacial period, on the other hand that during the Würm Ice Age it lived along the southern edge of the Nordic inland ice (in Jutland). Further, to the characteristics mentioned for *Simplocaria metallica*, it may be added in the case of *Elaphrus lapponicus* that this is one of the boreo-British species which also "hibernated" in the British Isles (Lindroth, 1935a).

In all the other species of the Fennoscandian fauna presumed to be Würm hibernators on the basis of more or less strong circumstantial evidence, we find only one or two pronounced characteristics of the recent area out of those established for *Simplocaria metallica*. It is advisable to arrange these species according to these characteristics.

a. Species with an isolated Fennoscandian area—chiefly to the east.

1. Total isolation of the entire Fennoscandian stock (less evident cases in parentheses):

742 (*Agonum consimile*)
(*Bembidion chaudoiri*)
B. dauricum
(*B. grapeioides*)
(*B. hyperboraeorum*)
B. lapponicum
(*B. prasinum*)
B. scandicum
B. siebkei
(*Dyschirius helléni*)
(*Nebria gyllenhali balbii*)
Trechus obtusus.

Part of the European subarea of *Agonum archangelicum* lying outside (east of) the region seems to be completely isolated as well.

2. Partial isolation, with a discrete subarea in the southwest (W) and/or in the north (N):

N	*Bembidion aeneum*
W	*B. argenteolum*
N	*B. femoratum*
W	*B. litorale*
W	*B. lunatum*
W	*B. minimum*
W	*Bembidion semipunctatum*
N	*B. transparens*
N	*Carabus nitens*
N	*C. problematicus*
W N	*Cicindela maritima*
W N	*Dyschirius angustatus*
W	*Perileptus areolatus*
N	*Pterostichus niger.*

3. Isolation only to the northeast, so that the possibility of a postglacial immigration from this direction is eliminated:

Amara interstitialis
A. lunicollis
Asaphidion pallipes
Bembidion grapei
B. saxatile
(*B. schüppeli*)
B. velox
Blethisa multipunctata
Bradycellus collaris
Dyschirius septentrionum
Harpalus winkleri
Notiophilus biguttatus
(*Trachypachys zetterstedti*).

b. Species whose assumed Fennoscandian interglacial stock is separated from a more southern located subarea (possibly the main area) by a more or less distinct gap ("zone of obliteration"), which cannot be explained on the basis of climatic or other existence factors. In addition to the species listed above under a(2):

Amara praetermissa
A. quenseli
Asaphidion pallipes
Bembidion schüppeli
Carabus coriaceus
C. violaceus (in Finland)
Dyschirius septentrionum (in Finland)
Nebria gyllenhali (in Finland)
Trichocellus cognatus.

743 c. Bicentric species:

Amara nigricornis ("tricentric" ?)
(*Bembidion fellmanni*)
B. siebkei
Carabus problematicus
Cicindela maritima
(*Cymindis vaporariorum*)
Dyschirius angustatus
D. helléni
(*Miscodera arctica*)
Nebria nivalis
(*Trichocellus cognatus*).

In the case of the 4 species in parentheses the gap may appear insignificant. But it lies in the well-explored province of Jtl and may therefore be real. The bicentricity is most evident in *Elaphrus lapponicus* (p. 741).

It is possible that these peculiarities of the map of one or other species of carabid may not convince the skeptic of a Würm hibernation in the Fennoscandian region. Before I go on, I would like to point out the evidence of wing-dimorphic species (pp. 366 ff.) and draw some inferences.

In the above-mentioned chapter (p. 415) it was—if I may say so—*proved*, that 7 species must be considered as Würm hibernators in the Fennoscandian region; for 2 more species a refuge along the eastern boundary of the region (on the White Sea) was assumed. The seven "certain" species are:

Bembidion aeneum
B. grapei
B. transparens
Bradycellus collaris
Notiophilus aquaticus
N. biguttatus
Pterostichus strenuus.

Some of these actually belong to characteristic distribution types, which are also represented by other, non-dimorphic species, and it might not be too bold to assume for these *by analogy* a largely identical history. The following groups may be excluded:

a. *Bembidion aeneum* type. A more or less isolated "refuge area" in western or northern Norway.

Bembidion minimum. The isolate in the Trondheim region cannot have arisen by upward migration into the eastern Norwegian valleys during the

744 Warm period, as was assumed for *Trechus discus* and *T. micros* (p. 689), because the species is bound to the seashore (p. 520).

B. femoratum. The homogeneous northern Norwegian subarea is isolated on all sides and represents an unambiguous interglacial relict (Lindroth, 1941, p. 438).

Carabus nitens. In Norway between latitude 66° and 69° N there are 7 localities which form a coherent isolate. The species is constantly brachypterous.

C. problematicus. Also constantly flightless. The northern Fennoscandian subarea (subspecies *strandi*) is also completely isolated to the east, since the species is unknown on that side of the Kola Peninsula.

Pterostichus niger. The isolate in northern Norway comprises just 2 localities, one of which is on the quite distant island 35 Hillesöy, where the species cannot have been displaced (p. 324). On the other hand the significance of the isolated localities of *Cicindela campestris* in the same regions is uncertain.

Trechus obtusus. The entire western Scandinavian area of this species, which is constantly brachypterous in our region, represents so to speak an expansion of the western Norwegian *Bembidion aeneum* area on all sides. The *Trechus* species has also crossed the Swedish border at four places.

b. *Bembidion grapei* type. The species included here might be considered as postglacial offshoots of a "Siberian" stock.

Amara interstitialis. No connection to the northeast.

A. nigricornis. Bi- (or tri-) centric. Concentration in the Veranger-Petsamo region.

Bembidion difficile and *B. prasinum*. Slight connection to the northeast.

Nebria gyllenhali. In the south there are discrete postglacial stocks, especially in Finland (Holdhaus and Lindroth, 1939, p. 270).

Notiophilus reitteri, *Patrobus septentrionis*, and *Pelophila borealis* show concentrations in one to three assumed refuges on the coast in the north, which are certainly not just apparent (and were discovered by more thorough exploration). *Patrobus* and *Pelophila* occur here as far as the outermost islands. *Notiophilus* is functionally brachypterous (dimorphic, but only one macropterous specimen is known).

In *Pterostichus adstrictus*, moreover, the poor connection to the northeast is noticeable.

c. *Pterostichus strenuus—Bradycellus collaris* type, distinguished by lack of
745 or very slight connection to the northeast, also by the distinct separation in the north between the Norwegian and Swedish stocks.

Amara aulica	*Leistus rufescens*
A. bifrons	*Pterostichus oblongopunctatus*
A. communis	*Trichocellus placidus.*
A. lunicollis	

Amara familiaris and *Harpalus latus* are doubtful; in the north they show a tendency toward synanthropy.

But there are other distribution types, which are not represented among the dimorphic species but seem to justify the assumption that at least part of the Fennoscandian area is to be attributed to "Würm hibernation" in light of certain cartographic peculiarities.

d. *The West Scandinavian type.* This comprises a few species that occur only in Norway, and in addition a large group whose members reach the highest latitudes along the Scandinavian west coast. This condition in most cases is no doubt climatically determined (pp. 474 ff.), and it is therefore not right to conclude "Würm hibernation" only on the basis of a wide distribution in Norway. On the other hand this is possible in species whose Norwegian stock encroaches into the Swedish region in places they would have reached more easily from the south—if the entire Scandinavian population is due to postglacial immigration. This is a proof that they lack a predominantly western distribution for climatic reasons.

Bembidion nitidulum has crossed the Swedish border toward the east, both in Jtl and in southern Lapland. The occurrence east of the Baltic Sea up to latitude 63° N shows still more clearly that it is not an "Atlantic" species.

B. virens. I earlier (Lindroth, 1935a, p. 624) showed the Norwegian origin of the Swedish stock, which immigrated down the rivers.

Carabus coriaceus. The Scandinavian area is very peculiarly split up. Since this largest carabid of our fauna cannot easily escape notice, the gaps on the map must be considered mostly real. This holds especially in its occurrence in
746 the eastern Mälar lake region. Here *Carabus coriaceus* is widely distributed and is even abundant at places in the Stockholm region south of the Mälar lake; on the other hand so far not a single individual has been found in southern Upl (it is found again only north of latitude 60°N and in northern Vst). This is a certain similarity with the distribution of *Hedera* (Fröman, 1944, pp. 663 ff.). The enigmatic distribution of this *Carabus* species seems to be understandable only in light of conditions *during the first half of the Littorina period* (Munthe, 1940, Plate XII; also Fig. 100, p. 702). The land namely emerged from the sea south of Stockholm much earlier than north of it, and the possibilities of a new colonization were correspondingly greater for a soil-bound species like *Carabus coriaceus*. It seems important to establish that these sections of the Littorina period fall in the atlantic period, when the climate was generally very humid.

That *Carabus coriaceus* is favored by a humid climate seems not only to be evident from its advance far north in Norway but namely is related to its mode of life. Its food consists chiefly of large snails (both[†]. . .) are bound

[†]A line seems to be missing in the original text, and a previous line is repeated in its place. From the biology of *Carabus coriaceus* (Part I, p. 532), the sentence may be reconstructed as follows: "(both *Helix* and slugs), which . . ." —Translator.

to forest, i.e. to a humid microclimate. Like *Carabus* (for instance, on the island of Hitra), in western Norway they live in more open situations (see, for instance, *Arion ater* in Økland, 1925, pp. 15 ff., Plate II).

One may therefore surmise that *Carabus coriaceus* enjoyed good opportunities of dispersal during the atlantic period and at that time colonized, among other places, the region south of Stockholm. The subfossil record near Dlr Skärsjö (p. 658) shows that at that time it was already present in central Sweden. During the following, generally drier sub-boreal, *Carabus* may have retreated deeper into the forests. These were adversely affected in the Bronze Age by the increased reclamation of land, so that the capability of dispersal of the carabid was curtailed.

Nevertheless, the most striking gap in the distribution of *Carabus coriaceus* is not the one here considered in Upl, but the one that separates the southern Swedish stock (in Skå, Hall[†] and possibly also Öld) from the more northern stock. I find this incomprehensible, unless we are dealing with two immigration groups. This means that the central Swedish stock should have come from the west, from Norway. This direction of migration has already
747 been established for *Amara montivaga* (p. 632); probably it was also true of *Harpalus puncticollis*. However, a postglacial immigration from the southwest directly to Norway seems inconceivable for the flightless *Carabus coriaceus*. Hence it must be assumed that *C. coriaceus* survived the last glaciation somewhere in the southern half of Norway.

Carabus hortensis may have had a similar history, but the almost uninterrupted Scandinavian distribution of this species does not show any separate stocks. Except the striking absence from the Jaeren Peninsula (Province 6) represents a gap.

Harpalus winkleri. North of latitude 64° N the western origin of the Scandinavian stock is quite evident all the more so since the species is not restricted to regions with an oceanic climate. The quite isolated solitary records in northeastern Fennoscandia are of enigmatic origin.

Leistus ferrugineus and *Patrobus atrorufus* are apparently favored by an oceanic climate, which, among other things, is evident from the lie of their northern boundary in Finland (p. 474). Nevertheless, the passes of the Scandinavian main watershed were crossed eastward by both species at several, sometimes similar places; they undertook a real invasion through the passes in central Jämtland, which in the *Leistus* species is distinctly limited to the south. Both are flightless and are undoubted hibernators along the Norwegian coast.

Trechus secalis, which is likewise constantly brachypterous, belongs to the same general distribution type and has certainly gone through the same

[†] A misprint in the original. Should be "Hll"—General Editor.

Fennoscandian history. Only in Jtl has it pushed east through the passes, and its western stock in Sweden has so completely merged with the southern stock that no distinction can be drawn. Nevertheless, it is noteworthy that the carabid is apparently missing from the well-explored region of Los (Hls) (the dot on the map in Part II was inserted out of a misunderstanding: see Supplement). A verification in nature of the ostensible record from 36 Nordreisa in the collection of Embrik Strand would be very interesting. If correct, it would show a hibernation even in the far north. At the same place *Nigritella nigra* has its only record locality in northern Fennoscandia (Holmboe, 1936).

Two particular groups, likewise western Scandinavian, among whose members Würm hibernators might be presumed, are the species concentrated in
748 southwestern or southeastern Norway, some of which especially in the former group, have a very small area. Its history is difficult to decide. Further information will be given in the following section on the disposition of Würm refuges.

e. *The alpine-subalpine type*, whose members are restricted to fjeld regions (and partly to tundra regions), has no representatives among the dimorphic species that might clearly reveal their history. In this connection, species occurring exclusively on the Kola Peninsula have been left out. We thus have three distribution groups:

1. Species distributed along the entire chain of fjelds:

Agonum consimile	*Bembidion hasti.*
Amara alpina	

2. More or less distinctly bicentric species:

(*Bembidion fellmanni*)	*Dyschirius helléni*
(*B. lapponicum*)	*Nebria nivalis.*
(*Bembidion siebkei*)	

Also *Elaphrus lapponicus*, considered above (p. 741). *Dyschirius angustatus* belongs partly geographically (but not regionally) to this group. The phenomenon of bicentricity is further discussed below (p. 752).

3. Northern Fennoscandian species:

Bembidion dauricum	*B. scandicum*
B. grapeioides	*Diachila arctica*
B. hyperboraeorum	*Nebria gyllenhali balbii.*

These 14 (16) species are undoubtedly Würm hibernators. Only one species, *Amara alpina*, seems to have an uninterrupted connection with regions east of the Würm ice, eastward through the Kola Peninsula. They cannot be southern postglacial immigrants for reasons discussed above (p. 710).

Other facts worth mentioning are: There are interglacial subfossils of *Agonum consimile, Amara alpina, Bembidion hasti*, and *Diachila arctica* from

749 Sweden (Lindroth, 1948a). *Nebria nivalis* (as a boreo-British species) has been found in Scotland—like *Amara alpina*—and hence must have lived during the interglacial period in Scandinavia (Lindroth, 1935a). Among the 6 strictly northern Fennoscandian species that could most plausibly be considered as postglacial immigrants (from the northeast), two are dimorphic. However, *Bembidion dauricum* occurs in our region exclusively in the brachypterous form, *B. grapeioides* predominantly in this form. *B. scandicum* is unknown outside the region and is the only species of carabid that is probably *endemic* to Fennoscandia.

f. *Bembidion schüppeli* and *Dyschirius septentrionum*. It is interesting that two species with such a complicated area map can coincide in all important features. The only important differences are, on the one hand, that only *Bembidion schüppeli* occurs in Denmark (Jutland, undoubtedly as an interglacial relict) and, on the other hand, that *Dyschirius septentrionum* is unknown at the White Sea, probably for lack of exploration. The ecology of the two species is largely identical (see Part I) and their history must have been the same.

In the southeast both species have a postglacial stock in Estonia and southern Finland, north as far as latitude 62°30′ N (*Dyschirius*) or 63°N. North of this there is a stock extending across northern Finland, which in the case of *Bembidion* (certainly also in *Dyschirius*) emanates from the east—from the White Sea. This immigration group, discussed above (p. 729), reached the Bothnian coastland and both species spread on the Swedish side south as far as Mdp; on the Finnish side only *Dyschirius* extends that far. Of the two stocks described, only in *Bembidion* is the western population, which hibernated in Norway, sharply separated (the single record of Lyl Gaskelought belongs here); in *Dyschirius* this western stock merged with the northeastern stock only in the far north. The difference is easily understood, since only *Dyschirius* is functionally macropterous. For the same reason all Swedish localities of *Bembidion* (with the exception of those in Lyl) are below the highest shoreline; they are so to speak coastal relicts and indicate an early immigration. *Dyschirius* advanced farther inland. The localities in Vrm certainly also belong to the western area.

g. Finally, as *Notiophilus aquaticus* type may be named the *pan-*
750 *Fennoscandian* species that have had the same colorful history as the above-mentioned species. In my opinion this is true of all of them. The area of a species that is distributed throughout Fennoscandia (considered geographically, not regionally) without perceptible gaps, cannot just be the result of postglacial immigration into the region or of hibernation within the region. We saw earlier what a short distance, with very few exceptions, the southern postglacial stock has advanced even in Sweden (p. 716) and the eastern one even in Finland (p. 718). There is no evidence to show that the

entire Norwegian coastland could have been colonized by any species that immigrated only postglacially. The most important demonstrable achievement of this kind seems to have been that of *Calathus erratus* (p. 377, Fig. 35), but it occurs in northern Norway only very locally.

Moreover there are astonishingly few "pan-Fennoscandian" species that really deserve the name, having reached the outermost limits of the Fennoscandian mainland in all directions. Most of the suitable species are missing along the north coast of the Kola Peninsula and in the farthest north of Norway. Besides *Notiophilus aquaticus*, strictly speaking there are only 2 pan-Fennoscandian carabids (br—brachypterous; in parentheses—dimorphic but macropterous specimens very rare, hence functionally brachypterous):

(br) *Calathus melanocephalus* br *Patrobus assimilis.*

If we relax the stipulation of uninterrupted distribution in the farthest north, the following species may also be called "pan-Fennoscandian":

(br)	*Agonum fuliginosum*		*Elaphrus cupreus*
	Amara apricaria		*E. riparius*
	Bembidion bipunctatum		*Harpalus quadripunctatus*
	B. rupestre		*Loricera pilicornis*
br	*Calathus micropterus*	(br)	*Notiophilus germinyi*
br	*Carabus glabratus*	(br)	*Pterostichus diligens*
	Clivina fossor		*P. nigrita*
br	*Dyschirius globosus*		*Trechus rubens.*

Other species have of course been found in all the "major regions" of Fennoscandia, but by the pronounced even if small gaps or other irregularities of distribution show that they have a double or multiple origin, and that the various stocks have still not merged.

751 *Amara brunnea*. Gap in northern Finland (north of the Arctic Circle).

A. praetermissa. Gap in central Sweden and on the Finnish west coast.

A. quenseli. Large lacunae in southern Sweden and central Finland, partly (but not consistently) as boundary against "*forma silvicola*".

Bembidion saxatile. See map (Fig. 116, p. 801).

B. velox. Large lacunae in southern Sweden and along the Norwegian coast. Concentration in northern Finland.

br *Carabus violaceus*. Gaps in central and northernmost Finland.

br *Cychrus caraboides*. Gaps in the inland of the north and at the Finnish west coast.

(br) *Cymindis vaporariorum*. Small but probably real gap in Jtl.

Dichirotrichus pubescens. (Only on sea with high salinity.) Gap on the Kola Peninsula.

Miscodera arctica. As in *Cymindis vaporariorum*.

Trichocellus cognatus. As in *Cymindis vaporariorum*.

It is most noteworthy that of these 31 widely distributed carabids of Fennoscandia (including *Notiophilus aquaticus* and *N. biguttatus*) 13, i.e. 42%, are functionally brachypterous. The corresponding figure for the Fennoscandian fauna as a whole, even if we consider all dimorphic species as brachypterous, is 99 species, i.e. 27%. The most widely distributed species in Fennoscandia generally have a poorer capability of dispersal! This is in complete contrast with the result (p. 435, Diagram 47) obtained by evaluating the relationship between flight capacity and total distribution of our species. It is the refuges, with selection in the Würm glaciation operating in favor of brachypterism, that are responsible for this converse situation in Fennoscandia.

I do not claim that every species mentioned in this section (pp. 738 ff.) must represent a Fennoscandian Würm hibernator. Undoubtedly it will be more prudent and objective to express the situation as follows: For each of these species the problem of a Würm hibernation should at least be seriously discussed.

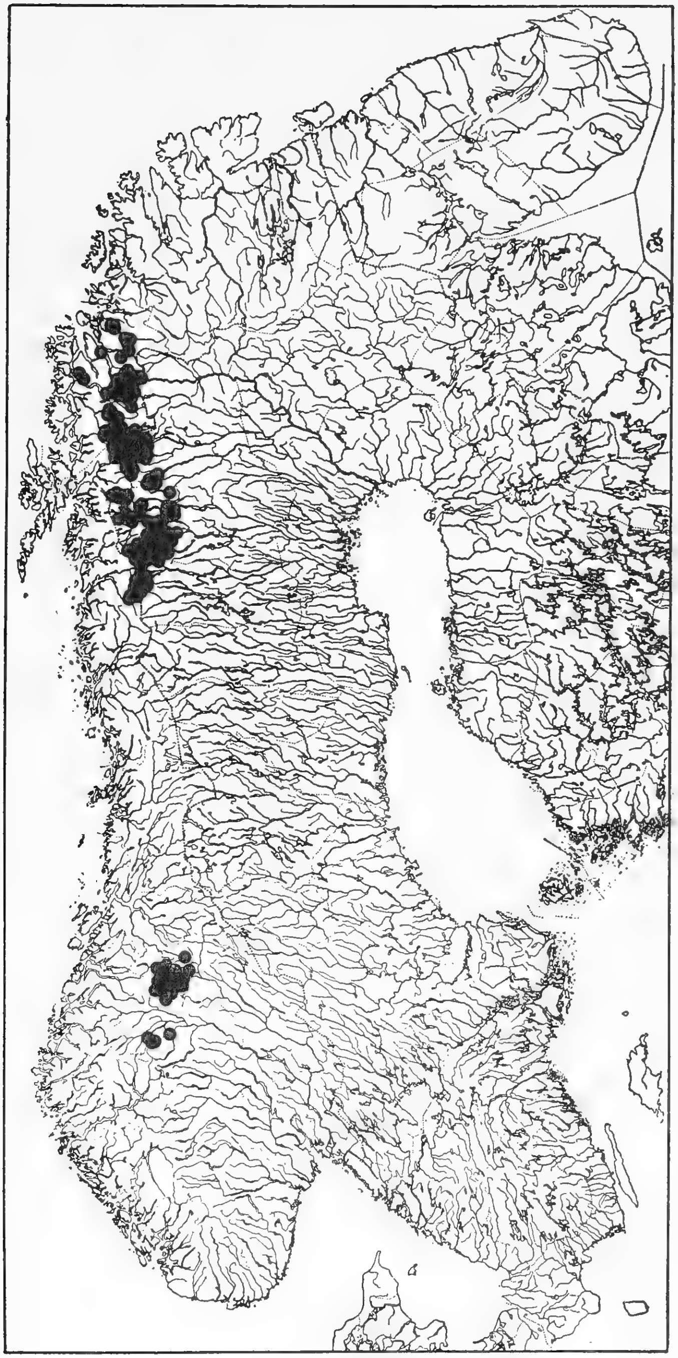
752 Table 38 (p. 802) provides a detailed survey not only of the species in question but also of the parts of Fennoscandia where the former refuge of each species might be envisaged.

II. Location of the Fennoscandian Würm refuges has been attempted by Nordhagen in particular (1933, 1935). However, earlier A.M. Hansen (1904, e.g. p. 299), Wille (1905), and especially Th. Fries (1913, p. 312) had already designated definite regions in southern and northern Norway that could be considered as refuges. According to these two Swedish authors, at least in the south the nunatak† regions, which were considered completely free from ice, would have played an important role besides any ice-free coastal stretches.

In locating the northern Würm refuges Th. Fries (1913) was able to draw on geological facts (Vogt, 1912; Enquist, 1913), but his most important source was the peculiar distribution of certain fjeld plants, and especially the marked *bicentricity* of some of them. As the word signifies, the area of a bicentric species has two "centers"—in the present case in the northern and in the southern part of the Scandinavian fjeld range—with a more or less broad gap or "zone of obliteration" in between. Species that occur in only one of these regions may be called "northern or southern unicentric" (Arwidsson, 1928). Collectively all the distribution types belonging to any of these categories may be called "centric" (Nannfeldt, 1947, p. 56). Two markedly bicentric species of different types are *Campanula uniflora* (Fig. 107) and *Saxifraga aizoon* (Fig. 108).

Simplocaria metallica is (p. 738; Fig. 106) a clearly bicentric beetle. Among the carabids there is no other case so clear. Nevertheless, bicentricity may be

†(cf. p. 736; suppl. scient. edit.).



753 Fig. 107. *Campanula uniflora*. (According to Arwidsson, 1943).

perceived in the 12 species listed above (p. 743), at least in the form of a small "zone of obliteration" in parts of Jtl.

In explanation of bicentricity there can be only one of the two causes: Either the area of the species concerned has split up under the influence of existence factors, or the gap is due to dynamical characteristics of the species, i.e. it is historically determined.

755 a. The view that the gap of a bicentric species may be due to climate (other existence factors scarcely figure), was argued early on (Th. Fries, 1913, p. 317; Tengwall, 1913, p. 268) and thereafter repeatedly cited as a useful reference. The "zone of obliteration" of the bicentric species always more or less coincides with the less pronounced high alpine central part of the Fennoscandian fjeld range, which, as clearly shown in the map in Fig. 61 (p. 437), is traversed by numerous wooded passes. It is quite possible that a species like *Nebria nivalis*, which is bound to the margins of perennial snowdrifts, would be excluded from the "gap" for climatic reasons (Lindroth, 1939a, p. 250; cf. also the temperature maps in Figs. 63–72, pp. 452 ff.).

These two authors (Th. Fries, Tengwall, l.c.) realized that the postglacial warm period may have fatefully affected the true alpine organisms in the lower central parts of the Scandinavian fjeld range. Later investigations by Hagem (1917) and others, but chiefly by Smith (1920, pp. 120 ff.) showed that the forest—mainly *Pinus*—extended into the fjelds up to 300 m (in southern Norway even up to 500 m, according to Hagem, (1917, p. 167) higher than now, a feature very clearly reconstructed in the central parts concerned (Hjd, Jtl). It is therefore conceivable that high alpine organisms in this region were destroyed during the warm period, and that thereafter there was no possibility of a recolonization of them.

b. On the other hand the above viewpoint cannot hold for non-high alpine or subalpine organisms or those living at still lower altitudes. This question was taken up by Björkman (1939). As a convincing example of a subalpine bicentric species he mapped the distribution of *Luzula parviflora* (l.c., p. 206). The Scandinavian fauna has only one carabid species, *Nebria nivalis*, so cold-requiring that the bicentricity may be due to climatic factors (today's or those of the warm period). That such an interpretation is impossible for the "model species" *Simplocaria metallica* too is seen at a glance from its distribution map (Fig. 106).

We therefore conclude that the more or less pronounced bicentricity in the Scandinavian distribution map of a number of carabids—with the possible exception of only *Nebria nivalis*—is not due to existence factors but to the history of the species.

756 It would be natural to interpret the subarea south or north of the gap as the result of a southern or northeastern postglacial immigration. But we have already (p. 713) declared a postglacial immigration of alpine-subalpine animals and plants from the south virtually impossible, which applies especially

754 Fig. 108. *Saxifraga aizoon*. (According to Holmboe, 1937).

to *Bembidion fellmanni* and *Nebria nivalis*. This is supported by the following facts.

Species completely missing from Central Europe:

Bembidion siebkei
B. virens
Dyschirius helléni
Elaphrus lapponicus
Nebria nivalis.

A southern postglacial stock in Scandinavia, separated from the south Scandinavian "center" by a more or less distinct gap, is shown by:

Cicindela maritima
Dyschirius angustatus
Trichocellus cognatus.

Amara nigricornis is not bicentric but "tricentric," as far as can be judged.

The distribution of the races of *Carabus problematicus* (map in Fig. 1, p. 21) shows that the southern postglacial stock is functionally separated from that of the southern "center" (*wockei*).

Only *Miscodera arctica* is left, whose southern contingent (down to southern Jtl) could well be the result of a southern postglacial immigration. I of course believe that the frequency and abundance of this species in the south Norwegian mountains (Fig. 56, p. 424) reveal a center determined not climatically but in the main historically.

Postulation of a northeastern (or southeastern) postglacial origin for the stock in the northern center of a bicentric species is ruled out by the fact that the area of many of these lacks any eastward connection, as far as is known (the Kola Peninsula is well explored!), or it is only poorly formed.

(*Bembidion fellmanni*)
B. siebkei
(*B. virens*)
Carabus problematicus
Cicindela maritima
Dyschirius angustatus
D. helléni
Elaphrus lapponicus
(*Miscodera arctica*)
(*Nebria nivalis*)
(*Trichocellus cognatus*).

757 Hence one can envisage at the most in *Amara nigricornis* and *Cymindis vaporariorum*, that the northern Fennoscandian "center" resulted from postglacial immigration from the east (northeast). However, the *Cymindis* species is functionally brachypterous and hence relatively slow to disperse.

We have found that the 12 more or less distinctly bicentric carabids of Fennoscandia cannot have achieved this characteristic of their area by postglacial immigration from the south, and from the northeast at most in two cases. The experience of botanists that bicentricity in the Fennoscandian mountains is to be attributed to a Würm hibernation in two separate refuge regions has general validity for the carabids (and other organisms) as well, a rule with more than solitary exceptions only among organisms that disperse very easily (see section on anemochorous dispersal, pp. 548 ff.).

Of the 12 carabids considered, 4 have never been found in the *Regio alpina* (Table 30, p. 440). They can therefore be termed at the most "subalpine;" they form good counterparts to *Luzula parviflora* (Björkman, 1939). For particular conclusions that can be drawn from this fact, see below (pp. 776 ff.).

The bicentric species allow us to identify two main refuge regions in Fennoscandia, one in the southwest and the other in the far north. Can these prospective large regions be more precisely located and perhaps divided into definite small refuges?

The attempt was made by Nordhagen on the basis of the disjunct distribution of the Scandinavian *Papaver* (1931; 1933, pp. 42 ff.), especially in his contribution of 1935 based on other fjeld plants as well. He thinks a whole series of definite relict species still grow only at localities where they must be assumed to have survived the Würm glaciation (or in their vicinity). In respect of North America, Fernald earlier drew attention to this "persistence" of some species of plants and to this conservative affinity for old localities. Later Hultén (1937, p. 22) used the term "rigid species" for them.

This rigid conservatism of some species in respect of locality is actually a real mystery (also emphasized by Holmboe, 1937, p. 28). It is not explained by
758 characterizing it, as Fernald does (for instance, 1925, p. 336; 1929, p. 1493),
as "ancient," "old," "conservative," "unaggressive," "nearly extinct."

It would be very useful to run accurate biological- and experimental-tests on several such "rigid" species of plant. It can be envisaged that their "conservatism" is due to one (or more) of the following four groups of characteristics:

1. *Poor capability of dispersal.*† The Leguminoseae, for instance, yield diaspores whose transportation is difficult. Even seeds of *Papaver* are not easily transported passively over long stretches. One would be inclined to envisage certain difficulties for the postglacial migration argued by Nordhagen, chiefly in the uphill direction from the south Norwegian coastal refuges (for instance, 1933, p. 46). Still, is it not conceivable that the hibernation of *Papaver* in southern Norway was at least partly on nunataks located farther inland? In Greenland a *Papaver* was found on the easternmost, most isolated nunatak of the "Jensen group" at a great height (Kornerup, 1890).

2. *Strong ecological specialization* (*stenotopy*). In the case of plants a dependence on limestone is evident here, as is emphasized repeatedly by Nordhagen (for instance, 1935, pp. 58, 92, 122), Holmboe (1937, p. 28) and others. It has adversely affected not only the "choice" of refuge but also the postglacial dispersal. According to Nordhagen the Würm hibernators among plants are generally more or less pronounced ecological specialists. Wynne-Edwards (1939) sees in this the whole explanation of their restricted distribution, which is certainly exaggerated.

†(cf. p. 823; suppl. scient. edit.).

3. *Poor competitiveness.* This characteristic is covered by Fernald's designation "unaggressive species," and great importance is attached to it by Nordhagen (for instance, 1935, p. 121).

4. *Reduced reproductive ability.* This on account of a sharp decrease in isolated populations during unfavorable periods, chiefly during the Würm hibernation. This purely quantitative variation can be combined with the fixation of disadvantageous mutations in Sewall Wright's sense (see p. 366).*

759 The above observations are not intended to detract from the importance of the distribution of plants as circumstantial evidence of a Würm hibernation or a more precise fixation of refuges. They only have to indicate that even in the case of species generally recognized as Würm hibernators, more investigations are necessary for us to formulate a more precise history.

In the case of our objects of study, the carabids, some of the conditions are simpler. Of the four above-mentioned groups of factors, competitiveness should of course be discounted (p. 554), and the dependence on limestone has at most a minor role (pp. 195 ff.). How far a decline in populations within the Würm refuges adversely affected the postglacial capability of dispersal, I certainly do not venture to declare in any particular case, but judge such an effect to be highly probable.

Undoubtedly the capability of dispersal through existing or lacking flight capacity has determined the size of the area colonized postglacially from the Würm refuges, as has been shown chiefly by the study of dimorphic carabids (pp. 335 ff.). In this way we can also help to contribute to the botanists knowledge in locating Würm refuges more precisely.

In the far north a refuge was assumed somewhere on the White Sea (p. 729) on the basis of entomological evidence. Conditions in the Finnish-Norwegian border region on the Arctic Sea coast point in the same direction (Petsamo-South Varanger). Nordhagen (1935, p. 130) thinks the assumption of a refuge on (or in the region of) the Fischer Peninsula is (botanically) useful and (geologically) possible. The distribution of the dimorphic *Bembidion transparens* supports this strongly (p. 389; Fig. 45). Moreover there is a whole series of carabids, whose distribution in the far north is most easily explained by postulating a refuge in the Petsamo-South Varanger region. Either they occur there more or less isolatedly or they are particularly frequent, which is not due only to the very thorough exploration of these regions. Examples are [br = brachypterous, (br) = dimorphic, but in the region concerned only or predominantly in the brachypterous form]:

760	*Agonum consimile*	(br)	*Bembidion grapeioides*
(br)	*A. fuliginosum*		*B. saxatile*
	Amara nigricornis		*B. velox*

*In this connection M. Fries (1949, p. 47) also speaks of "gene impoverishment" (Swedish: utarmande av anlag).

br *Carabus glabratus*
br *C. problematicus*
? *Cicindela maritima*
br *Cychrus caraboides*
Diachila arctica
Dichirotrichus pubescens
Dyschirius septentrionum
Elaphrus cupreus
E. riparius
Nebria gyllenhali balbii
(br) *Notiophilus reitteri*
(br) *Pterostichus diligens*
Trichocellus cognatus.

According to data supplied by Tanner (1937, pp. 104 ff.) it seems necessary to assume that the supposed refuge south of the Varanger fjord was located below the present sea level.

The existence of a Würm refuge on the Varanger Peninsula—or mainly on the present-day land below sea level to the north—is well substantiated geologically (Holtedal, 1929) and botanically (Nordhagen, 1933, pp. 69 ff.; 1935, pp. 116 ff.). However, entomologically these regions are so poorly explored that the question cannot be further discussed here.

The same is true of the assumed small refuges in Mageröy and at the mouth of the Porsanger fjord (Nordhagen, 1935, pp. 84 ff.). According to Nordhagen (1936, p. 113) the Mageröy refuge is now geologically proven as well. The coleopteran fauna here is extremely poor; from Mageröy, for instance, only 19 carabid species are known, and only in the case of *Carabus problematicus* can a Würm hibernation *in situ* be assumed.

The largest Fennoscandian refuge region during the Würm period is generally considered to be the coastal regions (today partly below sea level) from the estuarine zone of the Alta fjord (latitude 71°N), south to about the Arctic Circle (see, for instance, Fig. 106, p. 739). We may cite a whole series of geological evidences to show that the edge of the maximal Würm ice in some places, like the Lofoten islands, did not even reach the present-day outermost coastline (Vogt, 1912, pp. 6, 47; Enquist, 1913, 1918, pp. 5 ff.; Ahlmann, 1919, pp. 217, 238; Grønlie, 1927, p. 56; Nordhagen, 1933, pp. 20 ff.; 1935, pp. 136
761 ff.; Undås, 1939, pp. 181 ff.). On the well-argued assumption that the sea level at the Würm maximum was much lower than today (see also below), the extensive ice-free coastal regions along the above-mentioned stretch—as also numerous nunataks[†]—must have been available to the fauna and flora.

The carabids that must have survived the Würm period in this extensive refuge region form an imposing series. The following clear examples may be mentioned:

Asaphidion pallipes
br *Bembidion dauricum*
B. femoratum
(br) *B. grapei*
(br) *B. grapeioides*
B. hyperboraeorum
B. lapponicum
Bembidion saxatile
B. scandicum
(br) *B. schüppeli*

[†](cf. p. 736; suppl. scient. edit.).

B. siebkei
(br) *B. transparens*
(br) *Bradycellus collaris*
br *Carabus nitens*
br *C. violaceus*
br *Cychrus caraboides*
(br) *Cymindis vaporariorum*
Dichirotrichus pubescens
Dyschirius angustatus
br *D. helléni*
D. septentrionum
Elaphrus lapponicus
Harpalus quadripunctatus
H. winkleri
br *Leistus ferrugineus*
Miscodera arctica
Nebria gyllenhali balbii
N. nivalis
(br) *Pterostichus strenuus*
br *Trechus obtusus*
Trichocellus cognatus
T. placidus.

It seems hardly possible to pass a more precise judgment on which small refuge one or other species had hibernated. In the case of *Bembidion dauricum* and *Trechus obtusus*, both of which are constantly brachypterous, it must have been situated (completely or partly) in the region of the Lofoten archipelago.

On the other hand the carabids may contribute to fix the southern limit of this northern "major refuge." Originally Nordhagen (1933, p. 54) did not believe the southern refuges in northern Norway (at any rate not the floristically important refuges) to be situated more south than about the Arctic Circle (Svartis region); later (1935, pp. 139 ff.), in view of the southern record of *Arenaria humifusa*, he assumed small refuges to the south as far as Leka (latitude 65°N). The hatched region on my map (Fig. 50, p. 402; Fig. 106, p. 739) should therefore have, according to Nordhagen, a more southward extension.

762 But apparently a further adjustment in the same direction must be undertaken. The distribution of *Bembidion aeneum* (Fig. 49, p. 400), a dimorphic species, is obvious in this connection. It is known exclusively in the brachypterous form in its totally isolated west Norwegian area. Most of these record localities are in the gap between the "major refuges," and it is incomprehensible what should have caused this coastal species to migrate from the hibernation localities of the Würm period. It would be far-fetched, for instance, to consider the southern subarea (in Tröndelag) as originating from the Möre refuge. The two isolated west Norwegian record localities of *B. minimum* are situated on the Trondheim fjord as well. The southernmost localities of *B. lapponicum*, and to some extent the distribution of the flightless *Trechus obtusus*, point in the same direction, i.e. the assumption that there were coastal Würm refuges even in the "gap" between latitudes 63°30′ and 66° N. The geological evidence may also be cited in this connection. Both Grønlie (1927, p. 56) and Granlund and Lundqvist (1936, pp. 13–14) think that the outer islands of the Dönna group (latitude about 66° N) were not glaciated during the Würm. According to Undås (1934, pp. 55–57) the terminal moraines of the maximal Würm ice even in Tröndelag are situated on the mainland (Örlandet, northwest of Trondheim).

In southern Norway—south of the Trondheim fjord—three coastal refuges were assumed by Nordhagen (1933, p. 46); (a) Möre, (b) Sogn, (c) Ryfylke (Fig. 106, p. 739). In the first case he was able to rely on Kaldhol's geological findings (1930, pp. 96 ff.; 1931), according to which at least the outermost present-day coastal zone was not glaciated during the Würm period. The assumption of the two southern refuges was based on botanical evidence alone. According to Faegri (1940, p. 19) Jaeren seems to have been completely glaciated during the Würm period, only the island of Utsira may have been ice-free.

For southern Norway it is more difficult than for the far north to distinguish the "hibernators" with confidence, since in the case of species of the plains there has often been a secondary merging with postglacial stocks*; or the Scandinavian population as a whole may have immigrated postglacially. Only in exceptional cases is it possible to define the location of the actual refuge more precisely.

763 As examples of hibernators somewhere in southern Norway (south of latitude 64° N) the following may be mentioned:

Amara praetermissa
A. quenseli
Bembidion fellmanni
Carabus coriaceus
Cymindis vaporariorum
Elaphrus lapponicus
Miscodera arctica
Nebria nivalis
Patrobus septentrionis.

A few species with characteristic distribution offer an indication as to where their former Würm refuge (or that of several species) was situated.

a) In Möre, or at any rate in the coastal region between latitude 62° and 64° N.

Aëpus marinus
Bembidion grapei (Fig. 50, p. 402)
B. lunatum
B. siebkei
Carabus problematicus
Dyschirius helléni
Trechus fulvus.

It is possible that a few other species, of the *Bembidion argenteolum* type, have had the same history of hibernation (see p. 769). In my opinion this possibility must also be seriously considered for the oddly distributed rodent *Sicista subtilis* (cf. Ekman, 1922, pp. 206 ff.).

b) In the outer Sogn. The only species whose north Norwegian distribution points to this refuge is *Nebria nivalis*. It is noteworthy, on one hand, that it represents the only pronounced high alpine Fennoscandian carabid and, on the other hand, that the prime high alpine Fennoscandian fjeld region, Jotunheimen, is located just at the inner end of the Sogne fjord.

*Without race differences, for instance, it would have been difficult to distinguish the southern interglacial stock of *Carabus problematicus* (Fig. 1, p. 21).

In my opinion there is a causal connection here. Nordhagen assigned his refuges according to the distribution of alpine plants, in the case of Sogn almost exclusively in accordance with the isolated occurrence of *Papaver relictum* in Valders and along the inner Sogn (1936, p. 110). The essence of the especially disjunct distribution of the species he chose, is their poor capability of dispersal (p. 758). That they continue to live in their isolated relict localities, is the result of a long series of fortuitous circumstances. But especially these two:

1. During the last interglacial they must have lived in the vicinity of a developing refuge.

764 2. During the postglacial period they must have found a suitable biotope close to their refuge.

Both these facts are a matter of course. They lead to an equally simple conclusion: Distinct fjeld plants (of the "rigid" type) "hibernated" close to the present-day fjelds. In Scandinavia they may have already become "centric" (bi- or unicentric) during the last, partly quite warm (p. 673) interglacial period. This means that just as many (or more!) Würm refuges for pronounced alpine plants and animals are dependent on conditions before and after the hibernation, as from conditions in the glacial epoch itself. We cannot have a thorough understanding of the Würm refuges by a study of the alpine organisms alone.

Species like *Bembidion aeneum*, which can still live *in situ* within the limits of the refuge, are independent of the conditions in the adjacent inland. Their distribution is determined by the critical period of the glaciation.

Nebria nivalis and *Papaver relictum*, which must move with every change in the glacial situation, go through critical times during the transitional periods, and their distribution is the result of a favorable interaction between alternating refuges of opposite kinds: glacial refuges against interglacial refuges. If a "Würm botanist," equipped with sufficient geological knowledge, had undertaken an expedition along the ice-free stretches of the Norwegian coast, on discovering a rare *Papaver* or *Arenaria humifusa* he would have asked himself: "How has the poor plant been able to survive the severe interglacial period?"

I thus mean, that probably even along the southern half of the Norwegian west coast—as along the north coast—rather than a limited number of large Würm refuges (three according to Nordhagen) there must have been a whole series of small, ice-free stretches of land, more or less isolated from one another along the outer coastal belt. However, for reasons cited above, only a few were favorably situated in every way for the most pronounced "rigid" alpine plants to survive until today—their hibernation on the nunataks[†] farther inland excluded. In the case of *Nebria nivalis* at any rate hibernation on the nunataks in Jotunheimen appears to me more probable than in a coastal region at the mouth of the Sogne fjord.

765 c) In the extreme southwest, e.g. in Ryfylke. The most eminent botanical index is *Saxifraga aizoon* (Fig. 108, p. 754; Nordhagen, 1933, p. 53; Holmboe, 1937, p. 29).

A counterpart among the carabids is *Bembidion tibiale*, which in the whole of Fennoscandia has been found in only four localities close together in Ryfylke, where it is encountered constantly and partly abundant. Netolitzky (1929, p. 35) suggested that the isolated Norwegian occurrence of this species resulted from transport down the extended lower course of the Rhine and Elbe across the early postglacial "Dogger-land." This theory cannot be rejected out of hand, but it loses credibility for the following reasons:

1. "The insect is bound to a particular substratum, just as the phytophagous ones are bound to particular plants" (Netolitzky, l.c.), and this substratum consists of coarse material (rubble). For this reason the species is now missing from the lower course of the big West German rivers and nowhere reaches the North Sea coast (Horion, 1941, p. 129). It is still less likely that the species would be able to find suitable biotopes along the banks of the same rivers in the flat Dogger-land, where the gentle current was able to carry and deposit only the finest particles (silt).

2. The exact northward extent of the Dogger-land is not known. But in the postglacial period it cannot have been of the size Lewis pictured it to be (1935, p. 337), following the 85-fathom line. At any rate it was separated from Norway by the present-day Norwegian channel as a broad, deeply incised bay. If, in spite of this, *Bembidion tibiale* was able to cross this barrier (the insect is capable of flight) it would rather be expected on the banks of the southern Norwegian rivers.

3. *Bembidion tibiale* also occurs on the British Isles, even in Ireland, and it cannot have originated in the postglacial period. Like the "boreo-British" species (Lindroth, 1935a), *B. tibiale* indicates an older (interglacial) faunal connection between Scandinavia and the British Isles.

On the basis of the above discussion, *Bembidion tibiale* is to be considered as a Würm hibernator in southwestern Norway.

The situation is very different in the case of *Bembidion harpaloides*, which is known in Fennoscandia only from two localities: (2 specimens) in the *extreme*
766 *south* of Norway, which is exactly what one would expect following the dispersal from the Dogger-land. Besides, this species even today extends north as far as Hamburg on the North Sea coast, it was found even (as a "Dogger-land relict"?) on Helgoland (Netolitzky, 1916).

The contrary relationship between the two *Bembidion* species considered illustrates the great difficulty encountered in judging the specific southwest Norwegian faunal and floral element of Scandinavia. The possibility of a postglacial immigration across the sea must not be underestimated—whether in the Dogger-land period or later. In *Calathus mollis* (p. 369; Fig. 28) we had a clear example of this.

The following species may have reached southwestern Norway as "direct" postglacial immigrants:

Agonum marginatum
Amara lucida
A. quenseli (*"silvicola"*)
A. spreta
Bembidion pallidipenne
Bradycellus harpalinus
Calathus ambiguus
Cymindis macularis
Dromius angustus
Dyschirius impunctipennis
D. obscurus
D. politus
Nebria livida
Pterostichus aterrimus.

With the exception of the *Pterostichus* species, which in our region often occurs as an accidental migrant, all these species live more or less regularly along the sea as littoral or epilittoral species. A common characteristic is furthermore that they are winged, with the exception of the dimorphic (normally brachypterous) *Cymindis macularis*, which despite this we earlier (p. 287) found to be an insect with unusually strong capability of dispersal.

Among the Würm hibernators that survived the last glaciation in more northerly regions many (probably most) have a similar history in southwestern Norway. In the following species their long presence in the region seems clear from the recent distribution, partly according to the "dimorphic maps," (pp. 389 ff.) [br = constantly brachypterous; (br) = dimorphic, in the region concerned also in the brachypterous form]:

767 br *Aëpus marinus*
Amara nigricornis
Bembidion fellmanni
(br) *B. grapei*
B. hasti
br *Carabus glabratus*
br *C. problematicus*
br *Leistus rufescens*
(br) *Notiophilus aquaticus*
(br) *N. biguttatus*
(br) *N. germinyi*
Pterostichus adstrictus
(br) *P. strenuus*
br *Trechus fulvus*
Trichocellus cognatus.

It is striking that two-thirds of the species are functionally brachypterous.

Of much greater interest is the question: To what extent have species hibernated only in the southernmost Würm refuge of Fennoscandia? It is most probable that these should include the thermally most demanding members of the hibernation group, and that the evidence of their character as interglacial relicts may permit a judgment on climatic conditions during the Würm maximum. That question is discussed below (p. 791), and we will restrict ourselves here to the fairly clear cases.

Among the carabids, *Bembidion tibiale* (see below) is the best example. But the refuge character of the northern European area of *Chrysomela crassicornis* Hell. is still more clear-cut (Fig. 109). It too is restricted to the extreme southwest of Norway. It is a sluggish, soil-bound insect with rudimentary wings,

whose total area consists of small, scattered relict occurrences (Holdhaus and Lindroth, 1939, p. 206). It is inclined to the formation of races, since even the form native to the British Isles (including the Shetlands) is, according to Franz (1938), subspecific, different from the Norwegian *forma typica*. The small, concentrated Norwegian subarea, where the species is abundant at places, must be ascribed to a Würm refuge situated in this region. It is interesting to know that according to Faegri (1940, p. 19) the island of Utsira (west of Karmöy) may have remained ice-free during the Würm.

Among the carabids the following species may also be involved [br = constantly brachypterous; (br) = dimorphic, in the region concerned also occurring in the brachypterous form]:

	Agonum ruficorne		*Nebria brevicollis*
(br)	*Bembidion assimile* (Fig. 46, p. 394)		*N. salina*
(br)	*Calathus erratus* (Fig. 35, p. 376)	(br)	*Notiophilus palustris*
br	*C. fuscipes*	(br)	*Olisthopus rotundatus* (Fig. 32, p. 373)
(br)	*Carabus clathratus* (Fig. 38, p. 380)	(br)	*Pterostichus lepidus* (Fig. 37, p. 379)
769 br	*C. granulatus*	(br)	*P. minor* (Fig. 43, p. 388).

In the case of 7 dimorphic species the exclusive or predominant occurrence of the brachypterous form suggests that they occupied a refuge here. The three winged species occur more or less isolated in southwestern Norway. Of course, in connection with *Nebria salina* it was conceded earlier (p. 475) that present-day climatic factors *can* operate as in area limiting effect.

Before summarizing the results of the attempt to locate the Fennoscandian Würm refuges we must consider a group of species that have so far been ignored, of which *Bembidion argenteolum* may be taken as a typical example.

It is characteristic of this species that the center of its area is situated in the eastern part of the southern Norway. Hence its predominantly western distribution in Scandinavia is not the result of a predilection for an oceanic climate, which moreover is clear from its occurrence in the Baltic region southward down to the Karelian Isthmus. Ecologically in Scandinavia the species seems to be associated with the banks of the larger rivers (although also found on Lake Siljan in Dlr). But on the German Baltic Sea coast and in the Karelian Isthmus it also lives along the seashore (see map in Netolitzky and Meyer, 1933). On climatic and edaphic grounds it could no doubt live equally well on the duny shores of Skå, southern Hll or on Jutland. The noteworthy gap south of the Scandinavian area, which includes the whole of Denmark is therefore historically determined and precludes a postglacial immigration from the south.

Bembidion argenteolum in Scandinavia is an indubitable Würm hibernator, much as in the British Isles, where the species occurs exclusively along

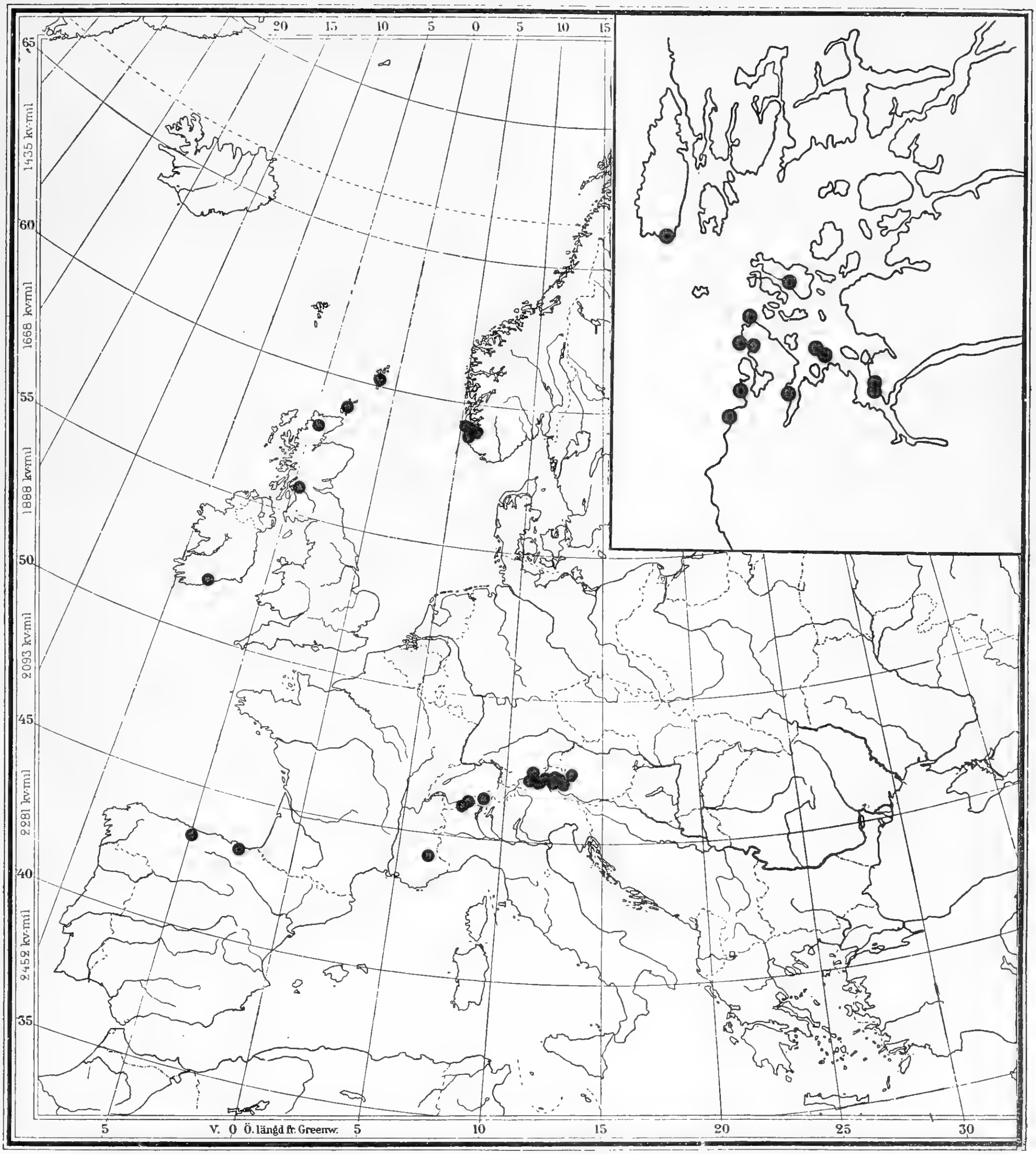
Lough Neagh in Ireland (concerning the erroneous report from England, see Lindroth, 1939a, p. 258). Like the remaining *Chrysobracteon* species it is a very conservative species (p. 590), which confines itself tenaciously to old habitable
770 regions. But where was its Würm refuge located? The occurrence in Tröndelag and in the upper part of the Gudbrands valley—among the generally accepted refuge regions of Norway—could indicate the coastal stretch between latitudes 62° and 64°N (hence the "Möre refuge").

B. semipunctatum has a Fennoscandian distribution nearly identical to that of *B. argenteolum*. The only difference is that with *B. semipunctatum* a postglacial stock reached Bornholm and the southern half of Skå. However, there the species nevertheless has the character of a vagrant migrant, which does not seem to live permanently at any locality.

On the other hand in the case of *Bembidion litorale* and *Cicindela maritima* the postglacial stock gained a firm footing in southern Sweden. But it is clear that the occurrence in central Scandinavia cannot be the result of an immigration by this route. The isolated Swedish occurrence in central Norrland must be explained, among other things, by an emigration from Tröndelag. Especially in the case of *B. litorale* any other explanation seems implausible.

We earlier (p. 601) emphasized the importance of hydrochorous transport by the large rivers. For instance, we explained the eastward dispersal of *Bembidion virens* in this way. In this species, which lives on coarse gravelly shores, there is a still clear connection between the localities at the Bothnian Sea and the Norwegian main area. On the other hand *Bembidion litorale* and *Cicindela maritima* are restricted to sandy and fine-sandy shores, which are not found on the upper course of the rivers concerned (Ljungan, Indals, Angerman). The enclaves in the Bothnian coastland therefore lack all connection with Norway today, whence they undoubtedly came, and we get a cartographic picture which in this context largely agrees with that of *Arabis petraea* (Holmboe, 1937, p. 23), a plant that has had the same history here. It is possible that the isolation catastrophes caused by the drainage of the large reservoirs of Jämtland at the end of the Finiglacial period caused the possibility of dispersal.

Both for *Cicindela maritima* and *Bembidion litorale* we are therefore inclined to assume a center of dispersal, a Würm refuge, in the Tröndelag-Möre range. But how are we to envisage the gap in the case of the latter species between Tröndelag and the more southern subarea (in southeastern Norway and Värmland)? The Gudbrands valley is one of the best explored parts of Norway and here the species is missing! Edaphically the river banks here are not unfavorable, as is evident from the distribution of the ecologically related species *Cicindela maritima, Bembidion semipunctatum, B. lunatum, Asaphidion*
771 *pallipes,* etc. I believe that *Bembidion litorale* here shows a historically determined gap, and that this stock in southeastern Norway-Värmland has a special origin, separately from the postglacial stock.



768 Fig. 109. *Chrysomela crassicornis Helliesen.* European distribution and the Norwegian subarea. (According to Franz, 1938, 1943a; Holdhaus and Lindroth, 1939; and according to Franz, Hinton, and Holgersen, *in litt.*). Exact position of the locality in northern Scotland ("Sutherland") is not known.

This assumption leads us to *Perileptus areolatus*. It must be conceded that this tiny insect easily escapes attention, and that the record in Hll somewhat strengthens the possibility of a postglacial immigration. But the Norwegian-central Swedish area, with its center in the vicinity of the Oslo fjord, altogether gives the impression of clear homogeneity. And why is the species missing not only from Denmark but also from the entire north German plain (Horion, 1941, p. 173)? Suitable biotopes[†] surely cannot be completely lacking. On the British Isles *Perileptus* lives exclusively in Scotland and Ireland, where it represents an unambiguous Würm hibernator; in the latter island it was found on the seashore, among others in the company of *Aëpus* (Halbert, 1937, p. 83).

In my opinion *Perileptus* is a Würm hibernator in Scandinavia too. But it does not occur within the limits of any of the generally accepted refuges considered above, and it cannot be that its recent area is due to emigration from any of these refuges. It is tempting to assume a refuge of the Würm period in southeastern Norway, in the vicinity of the outer Oslo fjord (emphasized earlier by Lindroth, 1939a, p. 257). "And it is very tempting to derive support from the opinion of the Swedish geologist Astrid Cleve-Euler [1946, p. 91], according to whom the so-called 'Raene,' the great terminal moraines at the mouth of the Oslo fjord (see Nordhagen, 1933, p. 124, and other studies), were actually formed by Würm ice at the time of its maximum extension" (*l.c.*). Of course this viewpoint might not be shared by other Swedish geologists.

The distribution of the sluggish, flightless curculionid *Otiorrhynchus salicis* Ström (Lindroth, 1939a, p. 255) would be much easier to understand on this assumption. And in general the plants and animals peculiar to southeastern Norway should be re-examined from this viewpoint, among other carabids those mentioned above (p. 687); also species like *Anthicus gracilis* Panz.

This is no place to do so. The hypothesis must obtain a stronger geological basis before we can begin a more detailed discussion. However, it may be
772 pointed out that during the Würm period the deep "Norwegian channel" at the coast, where undoubtedly large rivers emptied in these regions, may have caused an upward current of warmer water, which may have had a lococlimatically ameliorating effect (cf. the remarks by Elfstrand, 1927).

In conclusion the following remarks may be made on the location of the Würm refuges in Fennoscandia:

For high alpine plants and other organisms, hibernation is conceivable on the inland nunataks[††] surrounded on all sides by ice. In the present-day Fennoscandian *higher Regio alpina* only 5 carabids are endemic, of which at least in southern Norway nunatak hibernation is possible only for *Nebria nivalis*. In the Alps the nunataks have apparently played a much greater biological role (Lindroth, 1941, p. 439; Franz, 1943, pp. 505 ff.).

[†]"biotypes" in the original, evidently a printing error—Translator.
[††](cf. p. 736; suppl. scient. edit.).

Otherwise the Würm refuges were located in coastal regions. The two easternmost refuges, at the White Sea and in the Petsamo-South Varanger region, are well substantiated by the distribution of carabids, in the former case entirely based on it. In the extreme north botanical evidence indicates refuges in regions of the Varanger Peninsula and Mageröy.

Along the entire Norwegian west coast, from latitude 71° N to Jaeren, during the Würm period there seem to have been a whole series of big and small refuges. The difficulty in locating them exactly is that most of them were below the present-day sea level.

Using diverse premises the geologists, climatologists, etc. have come to the conclusion that the level of the ocean during the Great Ice Age must have sunk on account of so-called eustatic movement. Attempts have been made to estimate the vertical difference, chiefly by calculating the volume of water stored on the earth as ice (and so removed from the ocean). The figures obtained for the last glaciation are highly variable, for instance, between 88 and 93 m (Antevs, 1928, p. 81) and $<$ 275 m (Ramsay, 1930; but his figures seem to relate to the Greatest Ice Age); Enquist (according to Du Rietz, 1935, p. 228) reckons at least 200 m. Most of the estimates are around 100–150 m (Holtedahl, 1929, pp. 7, 9; Tanner, 1930, p. 298; Zeuner, 1945, p. 251; 1946, p. 129). This is meant to indicate the actual regression in comparison with
773 the present-day shoreline and the secondary transgression resulting from relief from the burden and elevation of the sea floor has been subtracted. Farrington (1945) obtained similar figures (120 m) while studying postglacial changes in the depth of the sea in Western Europe.

The *isostatic* movements, which for Fennoscandia as a whole signified a sinking under the pressure of inland ice, exercised little influence on the—in comparison with the ice cover—peripheral coastal regions in the extreme north and west, particularly in the central part of the west coast, in Tröndelag (Fig. 110). Moreover it must be remembered that the isostatic sinking that took place against the eustatic movement, on account of the inertia of the earth's crust, reached its maximum much later than the greatest extension of the Würm ice. We may be justified in reckoning about one-half the amount of the total isostatic sinking at that time (i.e. corresponding with the real postglacial elevation).

Keeping in view the isostatic and eustatic movements the following estimates may be attempted with regard to the lowest position of the coastline at the time of the Würm maximum:

Fischer Peninsula in Petsamo: 75 m.
North coast of Varanger Peninsula and Mageröy: 90 m.
Outermost coastline of Söröya to Röst: 100 m.
Coast between latitudes 67° and 63° N: 50–60 m.
Möre: 75–90 m.
Coast between Stad and Jaeren: 100 m.

These figures are probably minimal. Granlund and Lundqvist (1936, p. 14) estimated a level 200 m higher than now even for the Dönna region (latitude 66° N).

In the hypothetical map (Fig. 111) the outer, seaward limits of the refuges are drawn according to these figures. The inner (southern or eastern) limits (transversely hatched lines) wherever possible are based on the geological facts mentioned earlier. The division of the coastal foreshore into small refuges is based on the geomorphological structures of the land in that way that glacier tongues which reached the sea belt were assumed in the extension of the present-day fjords and valleys.

774 I have not attempted any kind of reconstruction of the White Sea refuge, still less the quite uncertain "Oslo refuge."

III. Climatic conditions during the last glaciation. In the synoptic Table 38,
776 (p. 802) altogether 97 Fennoscandian carabids (including one subspecies) are listed as Würm hibernators within the region (including the refuge at the White Sea). In addition there are 33 doubtful cases. In the case of 52 carabids (including the subspecies *balbii* of *Nebria gyllenhali*) postulation of such a hibernation seems unavoidable.

Let us now study the climatic requirements of these species, as evidenced by the present-day distribution of each species in the different plant regions of the region (Table 30, p. 440).

Of the 52 "undoubted" hibernators we have: in the *Regio alpina*: 30* (58%); *Regio betulina*: 46 (88%); *Regio coniferina*: 48 (92%).

Of the 45 "almost sure" hibernators: *Regio alpina*: 21 (47%); *Regio betulina*: 29 (64%); *Regio coniferina*: 45 (100%).

Of the 33 "possible" hibernators: *Regio alpina*: 6 (18%); *Regio betulina*: 7 (21%); *Regio coniferina*: 30 (91%).

So we find that 42–56% (22–73 species) of the Würm hibernators at present do not cross the timberline, and *apparently do not tolerate an arctic climate.* Moreover, a considerable number of these species occur more or less accidentally in the *Regio alpina* (see Tables 30 and 38). Is this fact compatible with the usual idea of the Ice Age climate?

The ultimate causes of glaciation need not be considered here. The views of the different authors, all hypothetical, offer glaring contradictions (see, for instance, Woldstedt, 1929, pp. 348 ff.; A. Wagner, 1940, pp. 145 ff.; Zeuner, 1946, pp. 134 ff.). But it is natural, at first glance inevitable, that a general decline in the atmospheric temperature should be taken as the secondary cause

*Not found in the Fennoscandian *Regio alpina* are the following "undoubted" Würm hibernators: *Aëpus marinus*, *Amara interstitialis*, (*Asaphidion pallipes*), *Bembidion aeneum*, (*B. femoratum*), (*B. grapei*), (*B. lapponicum*), *B. lunatum*, *B. nitidulum*, *B. saxatile*, *B. scandicum*, *B. schüppeli*, *B. siebkei*, *B. transparens*, *Dyschirius angustatus*, (*D. hellèni*), (*D. septentrionum*), *Leistus ferrugineus*, *Patrobus atrorufus*, *Pterostichus adstrictus*, *P. strenuus*, *Trechus fulvus*. Species in parentheses were found in the *Regio alpina* outside the region.

774 Fig. 110. Highest coastline (HK) of the postglacial period (*s. l.*) and isobases. According to Granlund, 1936.

of every ice age.

Calculation of the extent of this temperature fall during the Würm period had to be indirect, using chiefly the earlier position of the snowline. Most estimates envisage a fall of 3–5° C in comparison with the present-day tem-
777 perature of the region concerned (Antevs, 1928, p. 21; Woldstedt, 1929, p. 339), but Penck (1936) and following him Köppen and Wegener (1940, p. 22; also A. Wagner, 1940, p. 140) calculate the temperature fall for the ice-free parts

775 Fig. 111. Hypothetical map of Fennoscandian (and Danish) Würm refuges. Cross-hatching indicates maximum extent of Würm ice from south to north on geological basis.

Following sources were used: I—Kaldhol (1930); II—Undås (1934); III—Grønlie (1927), Granlund and Lundqvist (1936); IV—Vogt (1912); V—Enquist (1918); Grønlie (1927); VI—Nordhagen (1935, 1936); VII—Holtedahl (1929).

of Central Europe at 8° C. Mostly the annual mean temperature is cited, but at the same time it is often emphasized that a decline in summer temperatures is especially important for the development of glaciation (for example, Woldstedt, 1929, p. 340).

How then would a temperature decline of this order of magnitude in summer affect the fauna of the parts of Fennoscandia that remained ice-free during the Würm period? A study of the July isotherm map (Fig. 63, p. 452) shows that already with the smallest reduction postulated (3°C), the entire Norwegian west coast south to Stad (latitude 62° N) would incur an arctic climate, with the mean July temperature below 10°C. With the 8°C fall calculated by Köppen no part of Fennoscandia would have reached a mean temperature of +10°C in July!

Hence one must seriously ask whether the evidence provided by the "hibernators" among the carabids that are non-Arctic can be considered so conclusive. Could they not have changed their thermal requirements since the Ice Age? If not, do their relatively high thermal requirements not prove that they were no Würm hibernators?

In response to the first question it may be said that in some species we are probably justified in doubting the "constancy of the ecological valency," as Henriksen (1933, pp. 286 ff.) did in the case of *Otiorrhynchus dubius* Ström—although in this case perhaps erroneously. However, if we work with whole group of species whose members have identical requirements—in the present context thermal ones—the probability of a concurrent change in all of them can be taken as zero (see p. 676). Besides, it must not be forgotten that "adaptation" to a new climate does not represent a cumulative "acclimatization" from generation to generation, but must be due to genotypic changes (mutations), which are then subjected to selection. There is no reason to assume that such processes may take place concurrently in a whole series of species. Furthermore, what kind of selection would have resulted in the postglacial loss of "cold resistance" on the part of the populations that hibernated?

The second question, whether there are actually non-Arctic species for which Würm hibernation within the limits of Fennoscandia must be considered indispensable can be answered by referring to the species having wing
778 dimorphism. As far as I understand it, for some (at any rate for 7) of them hibernation in western and/or northern Fennoscandia is as decisively proven as can be possible using the "evidence" provided by biogeography. And among these very 7 species there are 3 that have never been found above or north of the timberline, which are thus pronouncedly non-Arctic.

So it is right to doubt the general validity of the temperature fall calculated for the Würm period by geologists and paleoclimatologists, asking two questions:

1. Is it not possible for a glaciation to occur as a result of climatic changes other than a fall in the summer temperature?

2. Can a decline in temperature of the Ice Age macroclimate not be offset at lococlimatically favorable places or at least be strongly moderated?

1. Expressed simply, glaciation occurs in the situation where there is more snowfall in winter than the amount of snow that melts in summer. A state of equilibrium can be shifted toward glaciation not only by low summer temperature but also by increased precipitation in winter.

There are some authors (for example, Scharff, 1899, p. 65 ff.; Brockmann-Jerosch, 1909, 1919) who consider increased snowfall the most important climatic factor responsible for glaciation (see also Antevs, 1928, p. 20). Enquist (1916) also believes the precipitation conditions have played a decisive role. Furthermore it may be pointed out that according to Hyyppä (1933, pp. 29 ff.; 1936, pp. 446 ff., p. 458) and Sauramo (1942, p. 281) the standstill of ice during the so-called Salpausselkä stage was mainly due to an increase in winter precipitation. Assuming that the glacial climatic changes had a global character, it must be stressed that the glaciations of the northern hemisphere in East Africa and southwest Asia apparently coincided with periods of abundant rainfall (for example, E. Nilsson, 1947, p. 169).

Nevertheless, the catastrophic retreat of the glaciers in most parts of the earth in recent decades provided us with important information on the relevant climatic determinants. Ahlmann in particular has dealt with this problem
779 in a series of articles. He finds that the regression of glaciers cannot be explained by a rise in the summer temperature: "The most important cause of the melting away... seems to have been an increased influx of heat through the atmosphere. In comparison with the accumulation season, the melting season is prolonged due to higher temperatures in autumn and spring" (Ahlmann, 1948, p. 320; translated). This agrees with the changes established for the Scandinavian climate of recent times (p. 641), which scarcely involve the summer. In Spitzbergen, where the glaciers have strikingly retreated, the summer temperature during the period in question has remained virtually unchanged. Of course, as emphasized by Keränen among others (1944, p. 55) and Ahlmann (1948, p. 307), this is partly due to the fact that "even in summer the heat is largely utilized for the melting of ice and glaciers" (Keränen, l.c.). But conditions in Scandinavia show that summer temperatures even in glacier-free regions have risen much less than spring temperatures.

The following conclusion seems to be justified: If the large-scale general disappearance of glaciers during the late present epoch is not (or is only slightly) to be ascribed to higher summer temperatures, but to a prolongation of the annual melting season, then it must be assumed that a general augmentation of the glaciers—a glaciation—can develop without any substantial fall in summer temperatures.

From *biological* premises (to use circular reasoning!) it is at any rate clear

that the decline of 8°C calculated by Köppen and Penck for Central Europe in the last glaciation may not have general validity. The Würm hibernation of plants and animals on Iceland, Greenland, and other Arctic islands (for literature see p. 758), which is supported by sound reasoning, would have been impossible in such conditions. The present-day climatically most favorable parts of Iceland and Greenland would have had a mean July temperature of +2 to 3°C and −1 to +2°C respectively (calculated by Vedrattan, 1925, and Böcher, 1938, p. 10). On biological grounds it seems as if the glacial temperature decline in the north was less than in Central Europe.

780 2. To understand the loco-climatical conditions at the edge of an inland ice, it is useful to proceed from similarly situated places of the present.

There are many good examples around the world of rich flora and the corresponding fauna spreading in the immediate vicinity of a large glacier. The best-known case may be the Malaspina glacier in Alaska (Russel, 1893; Wolff, 1915). There the forest not only approaches close to the ice edge: it even grows on the moraine-covered glacier on a surface of 50–60 km^2. A vivid impression of the luxuriant character of this "glacial forest" is provided by Russel's photograph (1893, p. XIV).

In New Zealand and in western Patagonia evergreen rain forest thrives close to large glaciers (Du Rietz, 1935, p. 228).

From eastern Greenland, Böcher (1938, pp. 312 ff.) describes several very rich plant localities in the immediate vicinity of ice. One of the richest localities, situated near Wiedemann fjord on a southern slope at an altitude of 300–400 m above sea level is completely surrounded by ice (see his Plate I). Yet, it harbors many species of a pronounced southern distribution type in Greenland. In southern Greenland, *Betula* also grows at a short distance from ice. Lynge (1934, p. 164) has observed a very rich plant locality in the northern island of Novaya Zemlya, situated between the edge of terrestrial ice and the sea on a southern slope only a few hundred meters broad.

The most vivid case I know of, is southeastern Iceland (Lindroth, 1931, pp. 541 ff.). From the sea the coast appears inhospitable. The enormous Vatnajökull—the largest glacier in Europe—projects more than 2000 m almost straight out of the sea, leaving in between only a narrow, gray belt of rock and sand. But inside the valleys, on the southern, protected slopes, there are green meadows and the birch forest thrives. It is of course low (< 3 m), but well covered with an abundant lower stratum, chiefly of the meadow type.

Such an oasis of organic life is Skaftafell, surrounded by the glacier on two sides, and on the other two by the totally sterile gravel fields of the glacial rivers, extending right down to the sea. The distance from the place photographed (Fig. 112) to the ice edge is 1200 m.

The insect fauna of Skaftafell is very rich, considering Icelandic conditions. Six species (1 Collembola, 3 Diptera and 2 Hymenoptera) are known
782 in Iceland exclusively from this place. And what is more important, this fauna

781 Fig. 112. Iceland. Skaftafell at Vatnajökull. In the background is Hvannadalshnukur (2199 msl), the highest point of Iceland. The distance to the ice edge is 1200 m, Photo by author: July 1, 1929.

also includes species such as *Philonthus trossulus* Gr., *Quedius umbrinus* Er., and the Homoptera, *Lausulus pseudocellaris* Fall. (*Deltocephalus distinguendus* Fall.), which, as far as can be judged, reached their present-day northern climatic limit in Iceland.

It would be a rewarding task to undertake a precise study of the local climate and microclimate of Skaftafell. However, at present, it is not known. The macroclimate, even for Icelandic conditions, is fairly unfavorable. The two nearest meteorological stations, located in rather open country closer to the coast, namely, Fagurhólsmýri and Hólar near Hornafjörthur (at a distance of 23 and 90 km respectively), have mean July temperatures of 9.9° and 10.0°C respectively (Vedrattan, 1925),—which is a summer climate, corresponding with that of the furthermost northern peninsula of Norway (Fig. 63, p. 452). In these regions of Scandinavia numerous species of the Skaftafell fauna are absent (among the carabids: *Bembidion bipunctatum*, *Pterostichus adstrictus*, *Trechus obtusus*), at least partly for thermal reasons. It must be assumed that the location of Skaftafell has produced an unusually favorable lococlimate.

The fauna and flora of Skaftafell in southeastern Iceland therefore prove not only that the direct vicinity of a large glacier can be without a climatically deleterious effect, but that such a situation even produces a thermally favorable condition in comparison with more open locations farther from the ice. There is no reason to assume, that the proximity of ice in itself would have had a different effect during the Würm period.

The loco-climatically advantageous position of Skaftafell and so of similarly situated places in a more glaciated region—in Greenland today and along the Fennoscandian coast during the Würm period—seems to be due to the following factors:

1. The landscape is very hilly and therefore has southern slopes with favorable exposure to the sun. The importance of a sunny location on "southern hills" and "southern slopes," especially in southern Sweden, for the development of a rich flora has been illustrated by Andersson and Birger (1912, pp. 52 ff.) with a series of apt examples. The temperature measurements by Frödin
783 (1915) and Krogerus (1937) represent attempts to express this thermal advantage numerically. It is hoped that someone will take up this question in the future in all its aspects.

2. Marginal mountains and the ice itself provide protection from the wind. The scattered *Betula* forests of Iceland clearly reveal the decisive role of the wind as a factor detrimental to the vegetation (Lindroth, 1931, p. 445), especially in the thermally determined peripheral regions. Secondarily, a tall, lower stratum thrives under the protection of the forest, and the two together support a rich insect life. We will later return to the question whether it is justified to assume a woodland vegetation in the Fennoscandian Würm refuges.

3. A glacier situated at a sufficient altitude produces descending winds

(Foehn-winds), which can bring about a considerable warming of the marginal regions. The frequency of these winds is determined besides the differences in level also by the size of the glacier concerned, i.e. by the constancy of the high pressure that builds up over it. In Greenland such warm Foehn-winds have long been known.

It is evident that during the glacial period we have to reckon with an almost constant anticyclone over the ice (Enquist, 1916; Woldstedt, 1929, p. 342). It is on this assumption alone that the loess deposition in Central Europe can be understood (A. Wagner, 1940, p. 141). So the thermal effect of the winds radiating out from nordic inland ice was determined entirely by altitude factors. Along the southern edge, in low-lying Central Europe, the ice was estimated to be only about 100 m thick (Kessler, 1925, p. 153). The northern winds therefore moved almost horizontally and could not show a Foehn character. On the contrary, they had a strongly cooling effect on the ice edge region (Kessler, l.c.; Woldstedt, l.c.).

Very different conditions prevailed in western Norway. The fjelds, which form the main Scandinavian watershed, are situated at a short distance from the coast. The mean inland altitude was increased substantially by ice during the Würm period, and we may reckon with a descent of 1500 to 2000 m over the few miles down to the coast. The air streaming out from above the ice must have regularly achieved the character of a descending wind. It had a warming effect.

As far as I can see this is the most important reason why the mean temperature decline of 8°C calculated by Penck for the last glaciation in Central Europe cannot be applied to western Scandinavia. The occasional winds
784 from other directions would not have provided any substantial thermal compensation in ice-free parts of Central Europe, especially since these parts were at that time situated farther from the coast (the Dogger-land at any rate was supra-aquatic), and the west winds were therefore cooled down on their way.

In Scandinavia the westerly winds moving in straight from the sea were thermally much more favorable as well. The Gulf Stream must have moved along the Norwegian coast even during the Würm period, for there can be no question of so great a land elevation that the almost 600 m deep Wyville-Thompson ridge between the Shetlands and the Faeroes would have hindered access to the North Sea. On the contrary, the assumed moderate land elevation of 100 m probably signified a thermal advantage for the coastland, since this brought it closer to the edge of the continental shelf and so closer to the warm Gulf Stream water (emphasized by Elfstrand, 1927). The Gulf Stream avoids ocean regions less than 200 m deep (Schott, 1926, p. 184).

Conclusion: During the last glaciation those parts of Europe that formed coastal belts below a high inland were climatically much favored, especially if

they had direct contact with the Gulf Stream. No region meets these requirements better than the Norwegian west coast (see also Dahl, 1946, p. 239).

It is therefore in no way contradictory to the "exact" natural sciences if the biologists take the view that in the Fennoscandian Würm refuges other organisms than the Arctic (alpine) ones have also survived the glaciation.

Recently the view has been expressed that the Norwegian Würm refuges were covered with forest (at any rate with trees of woodland-forming species). Lindquist (1948), in his studies on the variability of *Picea abies,* not only—so to say incidentally—named two treelike *Betula* species (*B. callosa* and *B. tortuosa*) as Scandinavian Würm hibernators, but also extends his claim to *Picea abies,* which in the form of his newly described "variety *arctica*" is said to
785 have hibernated along the Norwegian west coast probably in the south (along Storeggen) and in the north (along the Vesterålseggen).

The following objections can be raised against Lindquist's arguments:

1. The "variety *arctica*" is not sufficiently distinguished from the Central European "variety *germanica* Lindq." Both have smooth annual shoots but are said to differ in the cones. The trees with smooth shoots sporadically occurring also in southern Sweden "probably belong to the variety *germanica*" (p. 304). How far these indicate a postglacial immigration from the south or originate from plantation trees of Central European origin is left unresolved (p. 321). Is it not more probable that the character of "smooth annual shoots" represents a mutant occurring in different populations independent of the structure of the cones?

2. The "variety *arctica*" never occurs as a pure stand. However, the percentage component (somewhat <30) increases in Scandinavia northward and westward, and is therefore highest along the area limits. It is then not possible that the smooth shoots are the superficial manifestation of a physiologically effective mutation, which in the critical regions of the area limit have a markedly positive selection value? Lindquist's argument to the contrary (pp. 307, 332) is not very convincing.

3. The weightiest objection is of a purely phytogeographical nature. As shown by Lindquist's map (Fig. 3, p. 259) on the localities of the spruce material he investigated, he studied practically no record material from northern Finland. Therefore, the isolation of the Scandinavian "variety *arctica*," becomes completely problematic. It is quite conceivable that the northern marginal occurrences of spruce are characterized by a belt with more conspicuous "variety *arctica*," not only in Finland but also in Russia and farther east. Consequently it is impossible to deny that the "variety *arctica*" may have immigrated as a component of the large postglacial stock emanating from the east. It is not really astonishing, that this eastern type with hairy shoots managed to reach every population of the wintered "variety *arctica*" in western Norway postglacially, which according to Lindquist (p. 325) has to be assumed because as far as is known there are no pure stands of "variety *arctica*"? Is

this an example of long-distance aerial transport of pollen?

As important evidences supporting the assumption of a hibernation of
786 *Picea* in Scandinavia, Lindquist (p. 329) cites the distribution of two lichens living on spruce, *Cavernularia hultenii* and *Tholurna dissimilis*, which were studied in detail by Ahlner (1948). However, in examining the evidence provided by these lichens the following facts must be borne in mind:

1. Their actual distribution is not sufficiently known. Ahlner himself (p. 94) says of *Tholurna* that "the map provides only a broad picture of the distribution" (translated). *Cavernularia* was first (described and) discovered in Scandinavia in 1937. Not only was it unknown earlier, it is also absent from the entire older herbarium material (with the exception of an accidental fragment collected along with a specimen of another lichen; Ahlner, p. 171). The best specialists, for instance, Degelius, the author of the species, have not seen this lichen although they have assiduously collected in the regions (e.g. Tröndelag) where the species seems to be common. Of the 250 presently known localities of *Cavernularia* (l.c., p. 33), Ahlner himself discovered more than two-thirds (pp. 169–172). Under these circumstances, to claim that one is even closely acquainted with the distribution of *Cavernularia hultenii* in Scandinavia, or that conclusions on the history of immigration can be drawn therefrom, is hazardous.

2. Lichens are organisms with unusually strong capability of dispersal. This is evident mainly from their regular occurrence on erratic rocks (for instance, Degelius, 1936). Another example is the occurrence of some oceanic species in Finland (maps in Degelius, 1935). From this follows, that the area limits of the lichens are mostly pronounced existence limits. Hence the lichens are less appropriate as objects of the branch of biogeography that deals with questions of the history of immigration. Ahlner (p. 145) expresses himself more cautiously than Lindquist (e.g. p. 334) concerning the question of hibernation.

3. Lindquist (p. 330) indicates the possibility that *Cavernularia* probably "hibernated" in western Norway on rock (and not on *Picea*). His assumption seems indeed to be based on a misunderstanding (Ahlner, p. 143), since the species was observed only in one case, it seems accidentally (pp. 34, 171), on a stone in Tröndelag. On the other hand, from the same region there are at least 5 records on *Alnus incana* and *Sorbus aucuparia*. I do not know how much importance to attach to this situation. It should of course not be ruled out that in the eastern part of its area *Cavernularia* has become exclusively an in-
787 habitant of spruce for microclimatic reasons (humidity requirement), whereas it can occasionally live on other trees only in an oceanic climate. If only deciduous trees would occur in the refuges, the lichen would perhaps be content with them.

These critical remarks on the conclusions drawn by Lindquist (1948) (and Ahlner, 1948) concerning a Würm hibernation of *Picea* have been rather detailed. However, the question is most important. I do not mean to say cate-

gorically that spruce cannot have hibernated, but consider it improbable. I do not find it appropriate to draw such definite conclusions from the primary material available to Lindquist. A more precise fixation of the "variety *arctica*" is necessary—and for this, breeding experiments are indispensable. Lindquist's material is suitable only for a working hypothesis and nothing more.

One can easily imagine how it will be cited by the less critical biogeographers in the near future: "If spruce hibernated in the Norwegian refuges, then it must be assumed that even. . . " etc. They will envisage the refuges overgrown with stately coniferous forest.

Actually, so far no definite clue has also been produced to show that birch is a Scandinavian Würm hibernator. In this field, too, Lindquist is conducting an investigation in connection with which two preliminary maps, on *Betula tortuosa* and *B. callosa*, have been published in the *Picea* contribution (1948, pp. 21–22). Concerning these it can be stated first and foremost that they are incomplete. Among other things, the connection to the east is obscure. However, it must be conceded that these "species" are unusually difficult to map on account of their strong inclination to hybridize. The hibernation of these two *Betula* species is in itself a strong probability; from the botanical side nothing more can be said at present.

Perhaps entomology can be of help in solving this problem. The carabids indeed do not include any monophagous species associated (directly or indirectly) with particular trees; but such species do occur among other Coleoptera.

Curculio (*Balaninus, Balanobius*) *crux* Fbr. is a small but characteristically marked curculionid which does not easily escape the collector's attention. In
790 Fennoscandia it is restricted to an isolated area in the farthest north (Fig. 113). It is unknown in central and northern Russia as well as in Siberia. The species is widely distributed in Central Europe and is therefore in no way climatically bound to the far north. The southern postglacial stock has reached only Denmark, not Scandinavia, and in the east Latvia. *Curculio crux* is an undoubted Würm hibernator in northern Fennoscandia. It is bound to *Salix*, where the larva develops inside nematode galls (West, 1940–41, p. 578). However, it does not live on creeping dwarf willows but on tall, smooth-leaved species, in Denmark on *S. cuspidata*, in the north perhaps chiefly on *S. phylicifolia. Curculio crux* therefore shows that shrub-forming *Salix* species grew in the Würm refuges of northern Fennoscandia.

Rabocerus (*Salpingus*) *foveolatus* Ljungh is a heteromeran with a wider Fennoscandian area (Fig. 114). This species also lacks any connection to the east, being unknown in northern Russia and Siberia. In the south the southern postglacial stock has reached only Skåne through Denmark. In Finland it has advanced much farther, but there is a distinct gap in Finnish Lapland; the northernmost locality, which may belong to the southern area, is Lm Kantalaks. The conditions in Sweden clearly show that the species here is of

western origin; the east coast has not been reached at any point. The most densely colonized subarea is situated in northern Norway, north of latitude 68° N. *Rabocerus foveolatus* is an indubitable Würm hibernator in this region, probably also in more southern parts of the Norwegian coast. The species is associated with trees. It lives (as predator or as "commensal") in the galleries of ipids: in Central Europe, Denmark and southern Sweden on all kinds of deciduous trees, in the north, as far as is known, exclusively on *Betula* (but not *B. nana*), where it was discovered by Palm (*in litt.*) together with *Scolytus ratzeburgi* Jans. This ipid is likewise found right up to the northernmost part of Norway (Strand, 1946, p. 595). An ipid living on *Salix* does not occur in northern Fennoscandia. If *Rabocerus foveolatus* is recognized as a Fennoscandian Würm hibernator it can also be cited as evidence for the survival of tree-like *Betula*.

A similar case is mentioned by Strand (1946, pp. 24, 210), namely, of the staphylinid *Phyllodrepa vilis* Er., which lives in various insect galleries under the bark of trees and the more ragged bushes. In Fennoscandia this species
791 is known exclusively on the Norwegian west coast, but has been found there only from 6 Ryfylke in the extreme south to 35 Tromsö. Strand is certainly correct in noting (p. 24) that this range could have been produced neither by the feeding biology of the species nor by climatic factors, especially when the species in its total area is not bound to an oceanic climate. *Phyllodrepa vilis* too must be a Norwegian Würm hibernator.

It would be a tempting and ambitious task to monograph the fauna dependent on the Fennoscandian fjeld birches, their ecology and history. I also believe that a similar study of spruce insects could provide valuable evidence for or against Lindquist's view (1948). Here one has the advantage of being able to use Saalas' valuable study (1917, 1923a) "Die Fichtenkäfer Finnlands" (The Spruce Beetles of Finland)†.

According to the above discussion, considerable entomological and botanical factual material favors the assumption that the Fennoscandian Würm refuges at least in part had a non-Arctic climate. The findings of paleoclimatology do not preclude the idea. The refuges were apparently covered with birch forest in wind-protected places (also assumed by Björkman, 1939, p. 207; Du Rietz, 1942, p. 189), and they may have largely corresponded to the present-day *Regio betulina* of the fjelds.

The more or less sure hibernators among the carabids (p. 776) also include species that may be climatically still more fastidious, since they never extend into the *Regio betulina*. Among them there is one group of species which according to its total distribution seems restricted to the west coast of Europe and has to all appearances already found its climatic northern limit in the southern half of Norway. This is the atlantic (oceanic) element, to which

†(suppl. translator).

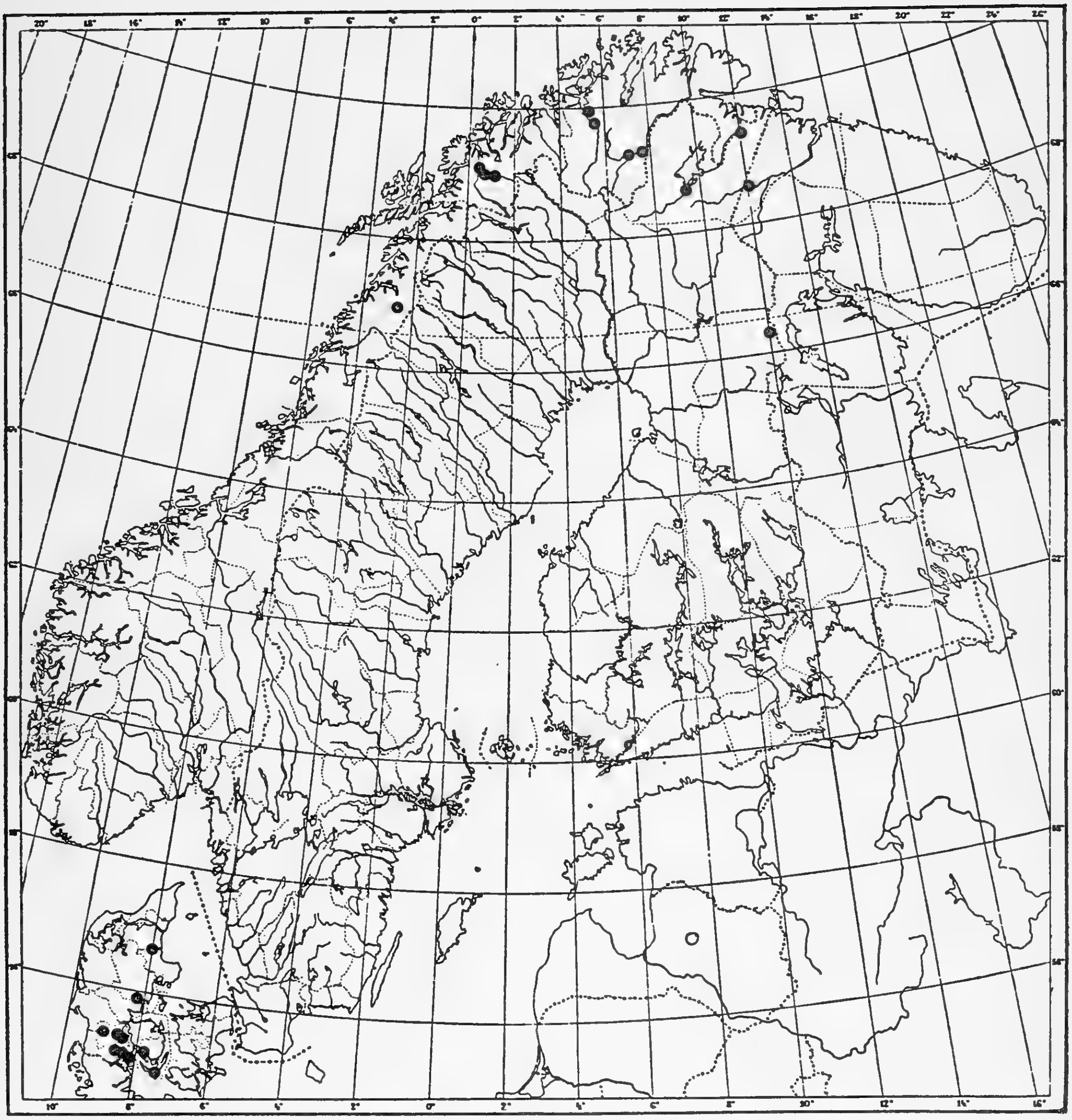
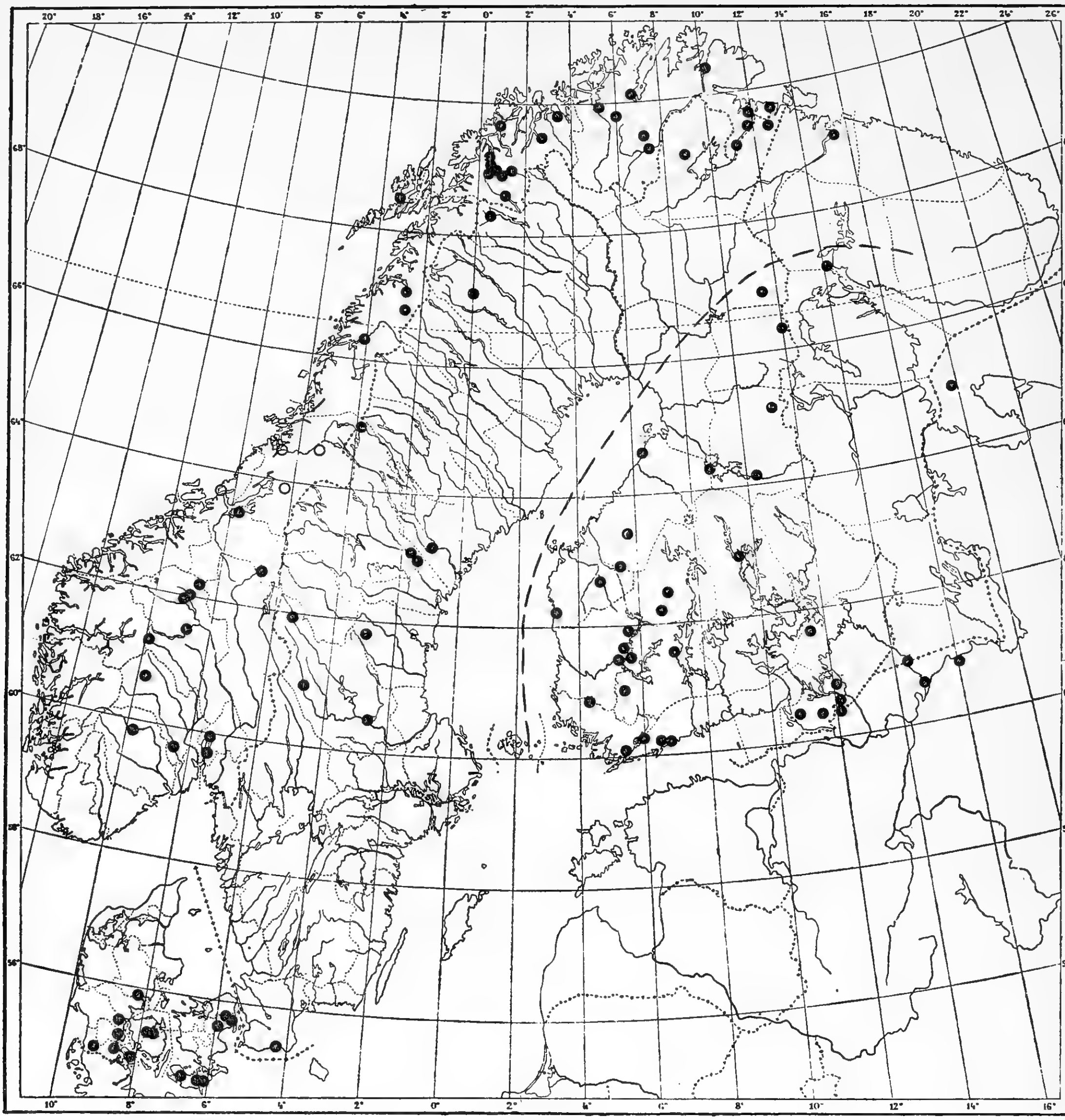


Fig. 113. *Curculio* (*Balaninus, Balanobius*) *crux* Fbr.



789 Fig. 114. *Rabocerus* (*Salpingus*) *foveolatus* Ljungh*. The assumed eastward limit of the postglacial stock is shown. Blank circles depict provincial finds in the Trondheim region. (According to Lysholm, 1937.)

*The localities of *Rabocerus foveolatus* have been compiled from the pertinent literature and from the larger public and private collections. It should be noted that the original description (from Småland) by Ljungh (1823, p. 269) may be applied equally well to *R. gabrieli* Gerh. (pointed out already by Seidlitz, 1920, p. 1108); Boheman's "*foveolatus*" from Små (probably Ölmestad, Anneberg, situated only 20 km from Ljungh's residence, Skärsjö in Billaryd) is also identical with *gabrieli* (RM!). So not only is Skå eliminated as a provincial find but also the name *foveolatus*. Even the record from Lyl Lycksele (Zetterstedt, 1840, p. 168), based on a damaged specimen (without anterior part of body) in ML, might refer to *gabrieli*.

correspond the most heat-requiring species of the so-called *Ilex* flora of the botanists.

Hence in determining whether a species is to be considered as part of the atlantic element, its total distribution must be taken into consideration. Like the curculionid *Barynotus squamosus* Germ., *Trechus obtusus* shall therefore rather be called "atlantic-alpine" (Lindroth, 1931, p. 555). *Bembidion tibiale* (p. 765), found only in Ryfylke, is likewise a montane species in Central Europe, whose occupancy of such a restricted Fennoscandian area is scarcely due
792 to climatic factors. In the present context, *Bembidion harpaloides* should also be omitted, partly because its occurrence in the extreme south of Norway was ascribed to postglacial immigration (p. 765).

As typical atlantic species there remain only *Aëpus marinus* and *Trechus fulvus*, which have almost identical distribution on the west coast of southern Norway, with the northernmost locality on the island of Hitra. Among other Coleoptera the two curculionids, *Otiorrhynchus porcatus* Hbst. (only in Province 7; total area less typically atlantic) and *Mesites tardyi* Curt. (only in Province 6) are the clearest corresponding examples. All 4 of these species occur on the British Isles.

It may seem rash to classify these animals (and the corresponding plants) as Würm hibernators, as I have already twice done (Lindroth, 1931, p. 554; 1932). Even the bold A.M. Hansen (1904, p. 57), who was otherwise far ahead of his time on these questions, did not venture to do so. Like Holmboe (1913, p. 90) later in respect of *Ilex*, he believed that the definite atlantic floral element had at least partly immigrated postglacially across the sea (probably with birds).

In recent years some botanists have been much more daring: they now entertain the idea of at least a partial hibernation of the "atlantic" species in Scandinavia (Degelius, 1935, p. 302; Du Rietz, 1935, pp. 228 ff.; see on the other hand Faegri, 1937, p. 437). The following facts may be cited in favor of this assumption in the present case:

1. It is not certain that the species restricted to southwestern Norway have here reached their climatic existence limit. Among the species considered above (p. 765), this cannot be so in the case of *Bembidion tibiale*, occurring solely in 6 Ryfylke, still less in *Corymbites cupreus* Fbr., also with an isolated occurrence there (map in Lindroth, 1939a, p. 248), which is in the process of invading Scandinavia from the east. The first specimen was found in the Swedish region in 1944 (Wirén, 1947, p. 191). Small isolated areas are not in themselves evidence for climatic relicts.

2. Of the 4 doubtful Coleoptera, 3 are constantly brachypterous (exception: *Mesites*). There is thus a limited capability of dispersal. That the terrestrial conditions postglacially, even during the Dogger-land period, were not favorable for a southern immigration directly to southwestern Norway has already been shown (p. 765).

793 3. *Trechus fulvus* also occurs on the Faeroes (on several islands) (West, 1930, p. 13), where it is undoubtedly to be considered a Würm hibernator.

4. The two carabids live on the seashore, right at the water, and are affected by the temperature of the seawater at least as much as by the "macroclimatic" atmospheric temperature. For reasons mentioned above (p. 783) the Gulf Stream exercised a strong thermal influence on the Norwegian coastland.

5. In the refuges of northern Norway species with pronounced thermal requirements (non-Arctic species) have overwintered as well (for example *Bembidion aeneum*, p. 399, *B. transparens*, p. 389, *Pterostichus strenuus*, p. 395, *Curculio crux*, p. 787, *Rabocerus foveolatus*, p. 790). At any rate the southern Norwegian refuges were climatically better situated; the insolation conditions were more favorable, and the Gulf Stream had still not lost its warmth. The south Norwegian refuges must have had a climate which at lococlimatically advantageous places was much warmer than subarctic (corresponding to the *Regio betulina*).

The two carabids (*Aëpus, Trechus fulvus*) have in my opinion to be considered as Würm hibernators, probably also at least *Otiorrhynchus porcatus*. With regard to the problem of the "*Ilex* flora" I am unable to provide any new point of view. It would perhaps seem strange if the above-mentioned *Mesites tardyi*, which in Ireland lives largely on *Ilex* (Munster, 1922, p. 131), had followed its host plant into a new country by postglacial "accidental dispersal." However, in Norway it was "unfortunately" found on *Fraxinus* (Munster, l.c.)! A detailed ecological study of the atlantic faunal element in Scandinavia will be a monumental, but certainly very rewarding task for some future zoologist.

In the absence of sufficient data from our own region we can turn to the conditions on the British Isles, where a prominent role is played not only by our atlantic element but in addition by a group of species with a more southern imprint, the so-called lusitanic group of species (Scharff, 1899, p. 287), which is native especially to Ireland and shows relationships with the Iberian Peninsula.

It is strange that on the British Isles—in many ways the most suitable region of Europe for this purpose—entomologists have shown relatively little
794 interest in biogeographical questions. The best synopsis of the Coleoptera has been provided by a foreigner (Sainte-Claire Deville, 1930a). In recent years, however, the British Lepidoptera have been the subject of a detailed zoogeographical study (Ford, 1945; Beirne, 1947b).

Beirne's contribution is an especially detailed analysis of the history of British macrolepidoptera, and represents an attempt to establish the time of immigration of every species. But his premises are extremely hypothetical; in particular, he rarely makes a serious attempt to explain the area of a species under the influence of the present-day environment. And indeed the Lepidoptera—with a few exceptions—thanks to their relatively strong capability of dispersal are well equipped to reach their existence limits in every climatic period (see also the Summary).

Especially interesting in the present context is Beirne's view (1947b, pp. 285–286) that certain "lusitanic" forms (in the families Noctuidae, Geometridae, Arctiidae), which are restricted to Ireland, represent the oldest element of the British lepidopteran fauna. He thinks it possible that they survived (also according to Scharff, 1899, p. 307) the maximum glaciation in Ireland* (or more correctly in a now subaquatic "foreland" south of it).

Even the botanists seem to be more and more inclined to assume the hibernation even of definite heatrequiring plants—including the lusitanic species—on the British Isles (Woodhead, 1929; Wilmott, 1930, 1935; Praeger, 1932; Degelius, 1935; Du Rietz, 1935b), at any rate during the last glaciation (according to the definition given by Wright, 1914, p. 76, and Charlesworth,
795 1929, p. 336, i.e. "New Drift" and Würm II in Movius, 1942, p. 26). Even the Outer Hebrides (or a foreland to the west of these) have been cited as a Würm refuge for characteristic southern species (Ford, 1945, p. 320; Harrison, 1947). There are not so many "counsels of caution" now as in the past, but they are still represented by Charlesworth (1930) and Salisbury (1935).

Among the relevant Coleoptera first and foremost is the flightless *Otiorrhynchus auropunctatus* Gyll., which is restricted to eastern Ireland and occurs outside the British Isles only in southern France and the Pyrenees (Scharff, 1907, p. 33). The above-mentioned, peculiar *Mesites tardyi*, which, outside the small Norwegian area, is endemic to the British Isles and is frequent only in Ireland, also belongs here (map in Scharff, 1907, p. 50). Its closest relatives are distributed from southern France over the western Mediterranean and on the Macronesian islands (Sainte-Claire Deville, 1930a, p. 104). *Mesites tardyi* cannot be a postglacial immigrant on the British Isles. It lives in decaying wood of *Ilex* and other deciduous trees (but has not been observed on *Betula*; O'Mahony *in litt.*) and hence points to the hibernation of "true" deciduous trees. This is imperative in the case of the pronounced American element in Ireland's flora (Praeger, 1932, p. 128).

There is therefore a whole series of facts that support a Würm hibernation of the pronounced southern species on the British Isles, including (a once larger) Ireland. Among these is the "lusitanic" element (see also Wilmott, 1935, p. 221), whose members, judging from the recent distribution, have greater heatrequirements than the corresponding "atlantic" group of Norway. Of course the present-day climate in Ireland is only slightly more favorable

*In respect of chronology, Beirne follows Movius' opinion (1942, pp. 26 ff.). He implies that the maximum glaciation ("Old Drift") of the British Isles was contemporaneous not with the Riss, but with the Würm I stage of the Alps and with the Warthe stage of northern Germany. Apart from the fact that the synchronicity of the Warthe stage and Würm I is quite uncertain (Richter, 1937, pp. 84, 126), it must be conceded that in all probability the maximum glaciation of the British Isles coincided with that of the continent (i.e. Riss and Saale respectively). Flint (1947, p. 343) synchronizes the Warthe stage with the first phase of the "Newer Drift" in Great Britain. However, in the biological context this question is of secondary importance.

than in western Norway (the mean July temperature in western Ireland is only 15°C; cf. Fig. 63, p. 452). If the glacial temperature decline in Western Europe was fairly uniform (which may be assumed at least for the parts affected directly by the Gulf Stream), the west Norwegian climate cannot have been much more adverse than that of the British refuges in the southwest and west.

In this indirect way we therefore arrive at the conclusion that even the pronounced "atlantic" organisms can have hibernated in western Norway during the Würm.

It also needs to be mentioned that during parts of the last interglacial
796 period the land in the present-day North Sea region was apparently situated higher than in any postglacial period (Lindroth, 1935a, p. 628). The land connection, which at that time allowed a dispersal of the "boreo-British" Coleoptera from Scandinavia to the British Isles, could also have been utilized by the "atlantic" species in the opposite direction—even if not at the same time.

If the climate and vegetation in the western and northern Fennoscandian refuges were the same as assumed here—if even in the far north at the most favorable places these refuges had a subalpine character with birch vegetation—then the conditions at any rate in southwestern Norway must have been much more favorable than in present-day Greenland. Undoubtedly all the preconditions were present to enable even man to live in the Fennoscandian Würm refuges (Ekholm, 1925). The fact that definitely dated remains of such a culture are not so far available is scarcely of decisive importance, since interglacial and "refuge" deposits within the region are extremely rare (Sandegren, 1948, p. 41). Moreover the latter—for reasons mentioned above (p. 772)—are to be sought largely on the present-day seabed. The so-called Komsa-culture on the Varanger Peninsula in the far north, considered by various authors (especially Nordhagen, 1933, pp. 82 ff.) as belonging to a Würm refuge age, was later (Bøe and Nummedal, 1936, pp. 183 ff.; Munthe, 1940, p. 220) classified as postglacial (s. l.). Only by definitely datable archeological findings can "the Fennoscandian Ice Age man" become more than a hypothesis. But it is a good and highly probable hypothesis.

The question whether some organisms survived more than one glaciation within the Fennoscandian region cannot be brought closer to a solution by a study of the carabids. The so-called west-Arctic element of the fauna and flora is relevant here, i.e. species whose Fennoscandian area indicates a former connection with the west, toward America. As far as is known there is no west-Arctic species among the carabids; even among the remaining Coleoptera there is so far no indubitable case known. On the other hand, the west-Arctic group among the Lepidoptera has a strength of at least 8 species (Wahlgren, 1919;
797 1935–1941, p. 54). The last list of the west-Arctic phanerogamic plants has been provided by Nordhagen (1935, pp. 143 ff.) and Nannfeldt (1940, p. 39).

The fauna and flora of the North Atlantic islands, particularly Iceland and Greenland, show that a direct, biologically effective land connection between Europe and North America did not exist during the last interglacial period (for example, Lindroth, 1931, pp. 567 ff.). It therefore seems we must shift the required "land corridor" into an earlier interglacial or even to the preglacial period. Such a view renders almost unavoidable the assumption that the west-Arctic species survived even the greater, penultimate glaciation (Riss) in Fennoscandia. It is certainly no accident that all the plants and Lepidoptera with pronounced west-Arctic distribution are able to live in the present-day *Regio alpina*.

Concluding Remarks on the History of the Fennoscandian Fauna

The most important characteristic of the Fennoscandian fauna is its youth. This characteristic has also been noted by Peyerimhoff (1947) in his lucid survey of the Danish-Fennoscandian coleopteran fauna (according to the *Catalogus*, 1939). Among the carabids there is at the most one species, *Bembidion scandicum*, which is *endemic* to the region. The beginning of the formation of an endemic subspecies is best shown by *Carabus problematicus*.

Moreover it is noticeable how even species that have lived in Scandinavia uninterruptedly since the last interglacial period have remained morphologically (taxonomically) unchanged, even when larger or smaller populations were isolated by the Würm Ice in separate refuges (Lindroth, 1941, p. 438). This is concrete evidence that even under strongly fluctuating environmental conditions, 100,000 years is not enough to produce new "species" in the family Carabidae. It is probable that this finding is also valid for other geographical regions.

Our fauna may not contain a Tertiary element, and even the possibility of continuous survival in Fennoscandia since the time of the greatest glaciation (Riss) cannot be ascertained for any species of carabid. Hence according to its origin, the Fennoscandian carabid fauna may be appropriately divided into three categories:

798 A. *Würm hibernators* (within the region).

B. *Southern immigrants*, which entered Scandinavia west of the Baltic Sea in the postglacial period.

C. *Eastern immigrants*, which entered Finland postglacially from regions east of the Baltic Sea (and in many cases advanced into the Scandinavian region).

A detailed synopsis on how to imagine the immigration route—or more often routes!—of each species is provided in Table 38. The many question marks betray our lack of certainty, and also the other data contain much that is subjective, especially with respect to the exact route of the postglacial immigration.

However, the main purpose of the Table is to emphasize the importance of *Würm hibernation*. Hence in the last four columns relating to this the "undoubted" cases are indicated by a bold cross, with page references to the text where our views have been substantiated.

Table 38 may be summarized as follows:

Würm hibernators*: 97 more or less sure species** = 27.1% of the entire fauna, of which

52 are "sure" species** = 14.5%
45 are "almost sure" species** = 12.6%
In addition there are 33 "possible" species** = 9.2%.

Southern immigrants: 280 more or less "sure" species = 78.2% of the entire fauna.

In addition there are 12 "possible" species = 3.4%.

Eastern immigrants: 266 more or less "sure" species = 74.3% of the entire fauna.

In addition there are 23 "possible" species = 6.4%.

799 Thus the Würm hibernators comprise at least one-fourth of the Fennoscandian carabid fauna.

It is striking that most of the species belong to more than one of the three main historical groups, i.e. they have a double or threefold origin.

Species with only one origin are:

5 (+1) = 6 Würm hibernators (1.7%)
55 (+1) = 56 southern immigrants (15.6%)
26 (+3) = 29 eastern immigrants (8.1%)
Total: 86 (+5) species = 25.4%.

Species with a double origin are:

4 (+3) = 7 species, which are Würm hibernators as well as southern immigrants (1.9%).

15 (+16) = 31 species, which are Würm hibernators as well as eastern immigrants (8.7%).

130 (+12) = 142 species, which are southern as well as eastern immigrants (39.7%).

Total: 149 (+31) species = 50.3%.

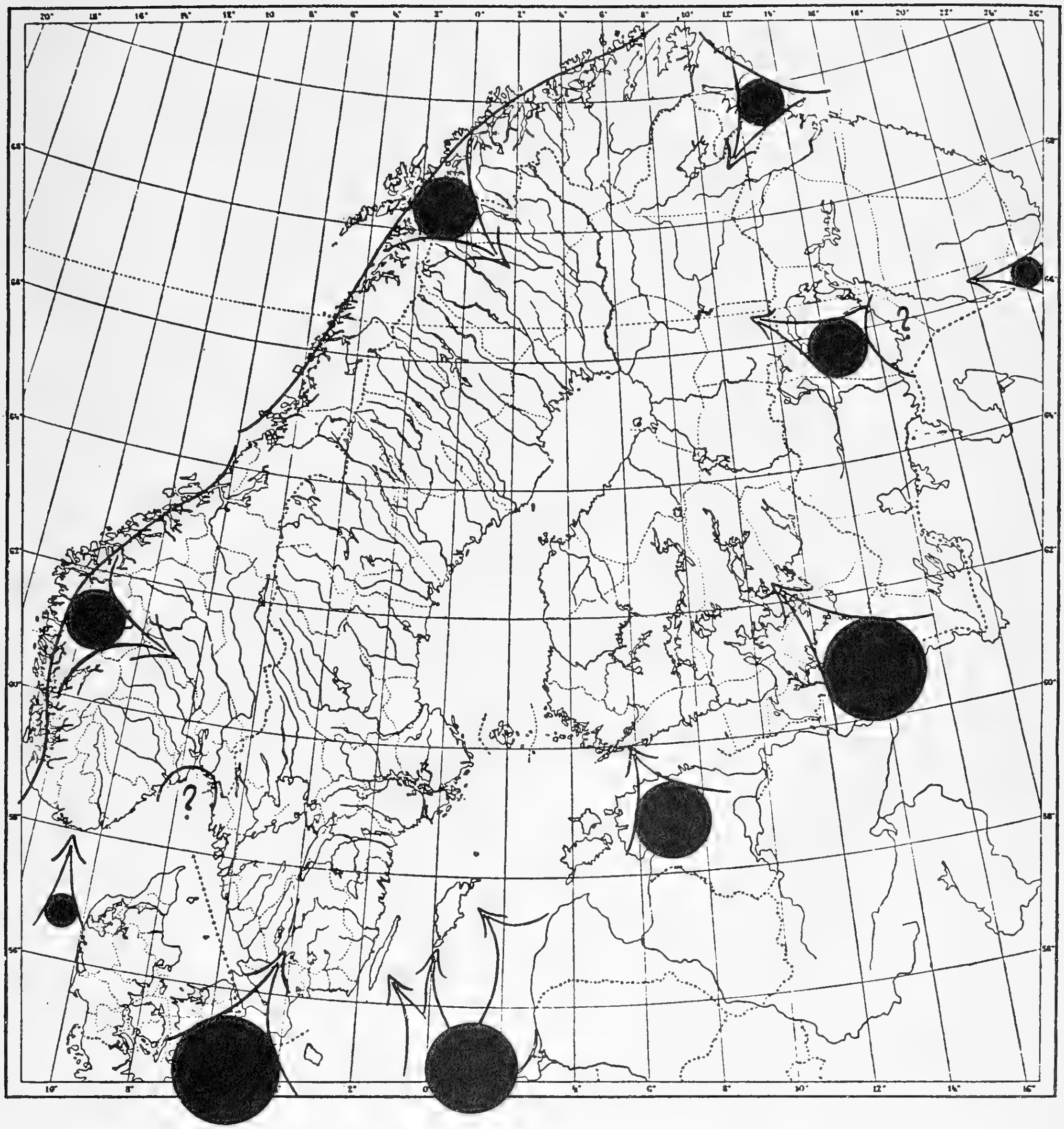
Species with a threefold origin, i.e. with Würm hibernation as well as southern and eastern immigration are:

58 (+29) = 87 species (24.3%).

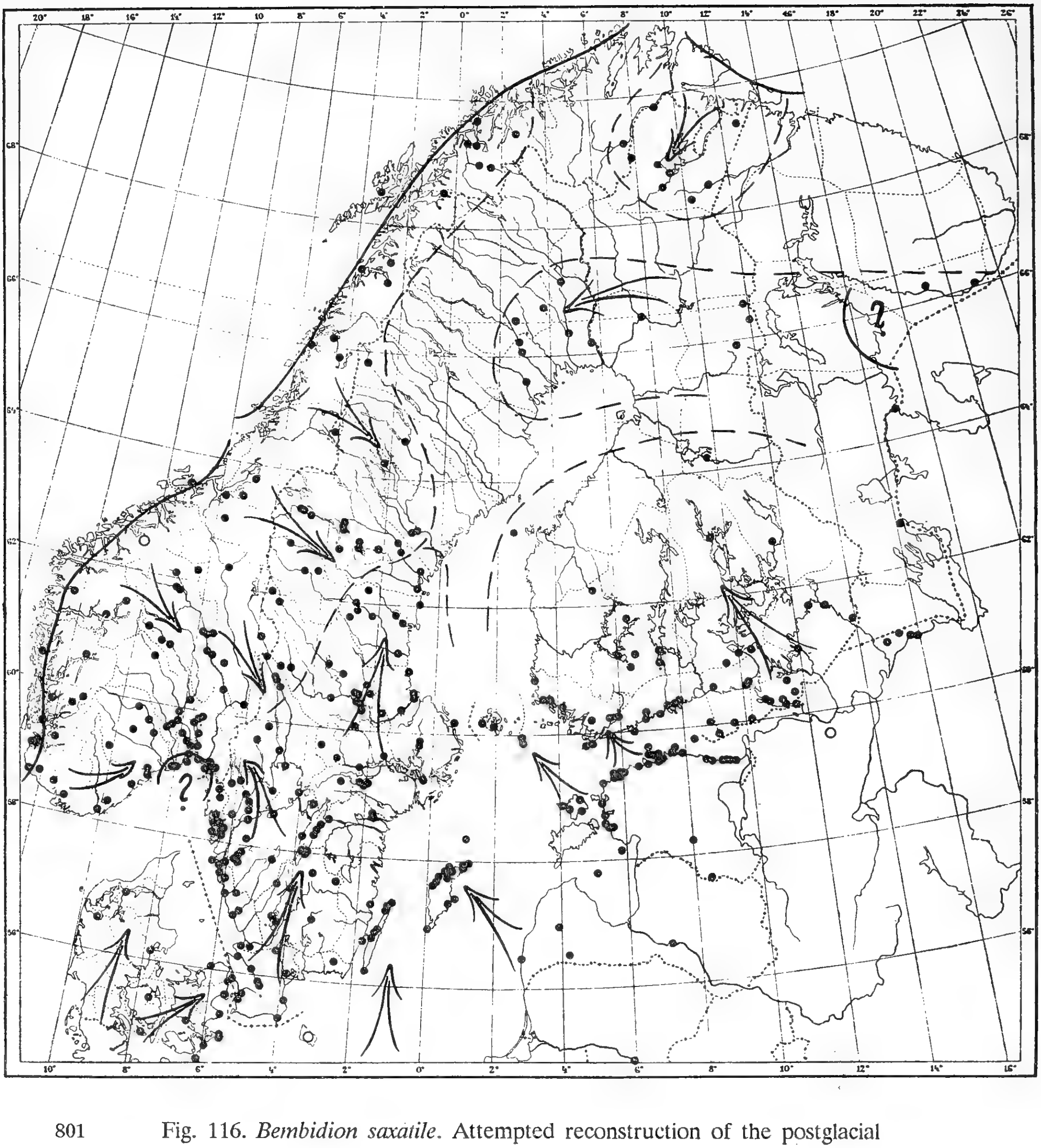
The map (Fig. 115) is an attempt to represent the contents of Table 38 cartographically.

*If the "hibernators" of the White Sea refuges (last column) are ignored the figures are: 94 more or less sure species (26.3%), of which 52 (14.5%) are "sure" and 42 (11.7%) "almost sure"; in addition there are 26 "possible" species (7.3%).

**Including the subspecies *balbii* of *Nebria gyllenhali*.



800 Fig. 115. Principal immigration groups of the Fennoscandian carabid fauna.
Cf. Table 38.



801 Fig. 116. *Bembidion saxatile*. Attempted reconstruction of the postglacial history of this species.

802 **Table 38. Postglacial immigration and migration of Fennoscandian Carabidae from Würm refuges. In the four "hibernation columns," which are of special interest, "sure" cases are marked with a bold cross**

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea[1]	
Abax ater	+	—	—	—	—	—	—	—	—	—	—	
Acupalpus consputus	+	—	+	+	—	—	—	—	—	—	—	To northern
A. dorsalis	+	—	+	+	+	—	—	—	—	—	—	Sweden directly
A. dubius	+	—	—	—	—	—	—	—	—	—	—	from Finland
A. exiguus	+	—	+	+	+	—	—	—	—	—	—	
A. flavicollis	+	—	?	+	+	—	—	—	—	—	—	
A. meridianus	+	—	?	+	?	—	—	—	—	—	—	
Aëpus marinus	—	—	—	—	—	—	—	**+**	—	—	—	p. 791
Agonum aldanicum	—	—	—	—	—	—	+	—	—	—	—	
A. archangelicum	—	—	—	—	—	—	?	—	—	—	+	
A. assimile	+	—	—	?	+	—	—	—	—	—	—	
A. bogemanni	?	—	—	—	+	?	—	—	—	—	—	
A. consimile	—	—	—	—	—	?	—	**+**	**+**	+	—	p. 741
A. dolens	+	—	—	?	+	+	—	—	—	—	—	
A. dorsale	+	—	?	+	—	—	—	—	—	—	—	
A. criceti	+	?	—	—	+	+	—	?	—	?	—	
A. fuliginosum	+	—	?	—	+	+	—	?	+	+	?	
A. gracile	+	—	+	+	+	?	—	—	?	—	—	
A. gracilipes	+	?	+	+	—	—	—	—	—	—	—	
A. impressum	—	—	—	—	+	—	—	—	—	—	—	
A. krynicki	+	—	+	—	—	—	—	—	—	—	—	
A. livens	+	—	?	+	+	—	—	—	—	—	—	Probably to
A. longiventre	—	—	—	?	—	—	—	—	—	—	—	Sweden directly
A. lugens	+	—	+	—	—	—	—	—	—	—	—	from Southeast.
A. mannerheimi	—	—	—	—	+	?	—	—	—	—	—	
A. marginatum	+	+	+	+	+	—	—	—	—	—	—	
A. micans	+	—	—	—	+	+	—	—	—	—	—	
A. moestum	+	—	+	+	+	—	—	—	—	—	—	
A. mülleri	+	?	?	+	+	?	—	—	—	—	—	
A. munsteri	?	—	—	—	+	+	—	—	—	—	—	
A. obscurum	+	—	+	?	+	—	—	—	—	—	—	
A. piceum	+	?	+	+	+	+	—	—	—	—	—	

[1]Perhaps in part immediately east of the Fennoscandian border.

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Agonum quadripunctatum	+	—	+	+	+	+	—	—	—	—	—	
A. ruficorne	+	?	+	?	+	—	—	?	—	—	—	
A. sexpunctatum	+	—	+	+	+	+	—	—	—	—	—	The three northern-most localities are uncertain or enigmatic.
A. thoreyi	+	—	+	+	+	—	—	—	—	—	—	
A. versutum	+	—	+	+	+	—	—	—	—	—	—	
A. viduum	+	?	+	+	+	?	—	—	—	—	—	
Amara aenea	+	?	+	+	+	—	—	—	—	—	—	
A. alpina	—	—	—	—	—	—	+	+	+	+	?	p. 748
A. apricaria	+	?	+	+	+	+	?	+	+	+	?	
A. aulica	+	?	+	+	+	?	—	+	+	—	—	
A. bifrons	+	?	+	+	+	—	—	+	+	—	—	
A. brunnea	+	?	+	+	+	+	?	+	+	+	?	
A. communis	+	?	?	+	+	+	—	+	+	—	—	
A. consularis	+	?	+	+	+	—	—	—	—	—	—	The finnish specimens are perhaps introduced.
A. convexiuscula	+	—	?	—	?	—	—	—	—	—	—	
A. crenata	—	—	—	?	—	—	—	—	—	—	—	
A. cursitans	+	?	?	?	—	—	—	—	—	—	—	
A. curta	+	—	?	?	+	—	—	—	—	—	—	
A. equestris	+	—	?	?	+	—	—	—	—	—	—	
A. erratica	—	—	—	—	+	+	+	—	?	?	—	
A. eurynota	+	?	?	+	+	+	—	—	—	—	—	
A. famelica	+	—	+	?	+	—	—	—	—	—	—	
A. familiaris	+	?	+	+	+	?	—	?	?	—	—	
A. fulva	+	?	+	+	+	+	—	—	—	—	—	
A. fusca	+	—	—	—	—	—	—	—	—	—	—	
A. infima	+	?	?	?	+	—	—	—	—	—	—	
A. ingenua	+	?	+	?	+	—	—	—	—	—	—	
A. interstitialis	—		—	—	+	?	—	?	+	+	—	p. 744
A. littorea	?	—	?	?	+	+	—	—	—	—	—	
A. lucida	+	+	+	?	+	—	—	—	—	—	—	
A. lunicollis	+	?	+	+	+	?	—	?	+	—	—	The entire Swedish stock from east across the sea.
A. majuscula	—	—	+	?	+	—	—	—	—	—	—	
A. montivaga	—	+	—	—	+	—	—	—	—	—	—	
A. municipalis	+	—	?	?	+	—	—	—	—	—	—	
A. nigricornis	—	—	—	—	—	+	?	+	?	+	?	p. 744
A. nitida	+	?	—	?	+	—	—	—	—	—	—	
A. ovata	+	+	+	?	+	?	—	—	—	—	—	

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Amara peregrina	—	—	—	—	—	—	+	—	—	—	—	
A. plebeja	+	?	+	+	+	—	—	—	—	—	—	
A. praetermissa	+	—	+	?	+	+	?	+	+	?	?	p. 742
A. quenseli	+	+	+	+	+	+	+	+	+	+	?	p. 742
A. similata	+	—	?	+	+	—	—	—	—	—	—	
A. spreta	+	+	—	+	+	—	—	—	—	—	—	
A. tibialis	+	—	+	+	+	—	—	—	—	—	—	
A. torrida	—	—	—	—	—	+	+	—	?	?	?	
Anisodactylus binotatus	+	—	+	+	+	—	—	—	—	—	—	To northern Sweden directly from Finland
A. nemorivagus	—	—	—	—	+	—	—	—	—	—	—	
A. poeciloides	+	—	—	—	—	—	—	—	—	—	—	To northern Sweden directly from Finland.
Asaphidion flavipes	+	—	+	+	+	—	—	—	—	—	—	
A. pallipes	+	—	—	—	+	?	—	?	+	—	—	p. 742
Badister bipustulatus	+	—	+	—	—	—	—	—	—	—	—	
B. bipust lacertosus	?	—	+	+	+	—	—	—	—	—	—	
B. dilatatus	+	?	+	+	+	—	—	—	—	—	—	
B. peltatus	+	—	+	+	+	—	—	—	—	—	—	
B. sodalis	+	—	+	—	+	—	—	—	—	—	—	
B. unipustulatus	+	—	+	+	—	—	—	—	—	—	—	
Bembidion aeneum	+	—	?	+	—	+	—	+	+	—	+	pp. 399, 762
B. andreae polon.	+	—	+	+	+	—	—	—	—	—	—	
B. argenteolum	—	—	—	—	+	—	—	+	—	—	—	
B. articulatum	+	—	+	+	+	—	—	—	—	—	—	
B. assimile	+	+	+	+	—	—	—	?	—	—	—	
B. azurescens	—	—	—	—	+	—	—	—	—	—	—	
B. biguttatum	+	—	—	+	+	—	—	—	—	—	—	
B. bipunctatum	+	?	?	+	+	+	?	+	+	+	?	p. 750
B. chaudoiri	—	—	—	—	—	—	—	—	—	—	?	
B. clarki	+	—	+	—	—	—	—	—	—	—	—	
B. crenulatum	—	—	—	—	—	—	+	—	—	—	—	
B. dauricum	—	—	—	—	—	—	—	—	+	—	—	p. 761
B. dentellum	+	—	+	+	+	—	—	—	—	—	—	
B. difficile	—	—	—	—	—	?	?	+	+	+	?	p. 744
B. doris	+	?	+	+	+	+	—	—	—	—	—	
B. Fellmanni	—	—	—	—	—	—	?	+	+	+	?	p. 743
B. femoratum	+	?	+	?	+	?	—	?	+	—	—	p. 744
B. fumigatum	+	—	—	—	—	—	—	—	—	—	—	

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea[1]	
Bembidion gilvipes	+	—	+	+	+	—	—	—	—	—	—	
B. grapei	—	—	—	?	?	?	—	+	+	+	—	p. 401
B. grapeioides	—	—	—	—	—	—	?	—	+	+	—	p. 741
B. guttula	+	—	+	+	+	+	—	—	—	—	+	
B. harpaloides	—	+	—	—	—	—	—	—	—	—	—	
B. hasti	—	—	—	—	—	+	+	+	+	+	?	p. 748
B. hirmocoelum	—	—	—	—	+	—	—	—	—	—	—	
B. humerale	+	—	+	+	+	—	—	—	—	—	—	
B. hyperboraeorum	—	—	—	—	—	?	+	—	+	?	?	p. 741
B. illigeri	+	—	+	+	—	—	—	—	—	—	—	
B. lampros	+	?	+	+	+	?	—	?	—	—	—	
B. lapponicum	—	—	—	—	—	—	—	?	+	?	—	p. 741
B. litorale	+	—	—	—	+	+	—	+	—	—	?	
B. lunatum	+	—	?	—	—	—	—	+	?	—	—	p. 763
B. lunulatum	+	—	?	—	—	—	—	—	—	—	—	
B. minimum	+	?	+	+	+	—	—	—	+	—	—	
B. monticola	—	—	—	?	+	—	—	—	—	—	—	
B. nigricorne	+	—	—	?	+	+[1]	—	—	—	—	—	
B. nitidulum	+	?	—	—	+	—	—	+	+	—	—	p. 745
B. obliquum	+	?	+	+	+	+	—	—	—	—	—	
B. obtusum	+	—	+	—	—	—	—	—	—	—	—	
B. octomaculatum	+	—	+	+	—	—	—	—	—	—	—	
B. pallidipenne	+	+	+	—	—	—	—	—	—	—	—	
B. prasinum	—	?	—	—	—	?	—	+	+	+	?	p. 744
B. properans	+	—	+	?	+	—	—	—	—	—	—	
B. punctulatum	—	—	—	—	+	—	—	—	—	—	—	
B. pygmaeum	—	—	—	+	+	—	—	—	—	—	—	
B. quadrimaculatum	+	—	+	+	+	?	—	—	—	—	—	
B. quinquestriatum	+	—	?	—	—	—	—	—	—	—	—	
B. repandum	—	—	—	—	—	—	?	—	—	—	+	
B. ruficolle	?	—	—	—	+	+	—	—	—	—	+	
B. rupestre	+	?	+	+	+	+	—	+	+	?	?	
B. saxatile	+	?	+	+	+	+	—	?	+	+	?	p. 801
B. scandicum	—	—	—	—	—	—	—	—	+	—	—	p. 749
B. schüppeli	?	—	—	+	+	+	—	+	+	?	+	p. 749
B. semipunctatum	+	—	—	+	+	—	—	+	—	—	—	
B. siebkei	—	—	—	—	—	+	—	+	+	?	?	p. 742

[1]Apparently immigrated on a more southern route.

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Bembidion stephensi	+	—	—	—	+	—	—	—	—	—	—	
B. striatum	—	—	—	+	+	—	—	—	—	—	—	
B. tibiale	—	?	—	—	—	—	—	+	—	—	—	
B. tinctum	—	—	—	—	?	+	—	—	—	—	?	
B. transparens	—	—	+	+	+	+		—	+	+	+	p. 389
B. unicolor	+	—	?	?	+	—	—	—	—	—	—	
B. ustulatum	+	—	?	?	+	—	—	—	—	—	—	
B. varium	+	—	+	+	—	—	—	—	—	—	—	
B. velox	?	?	+	?	+	?	—	?	?	+	?	
B. virens	—	—	—	—	—	+	—	+	+	+	?	p. 745
Blethisa multipunctata	+	?	+	+	+	?	—	—	?	?	—	
Brachynus crepitans	+	—	+	?	—			—		—		
Bradycellus collaris	+	?	+	+	+	+	—	+	+	—	?	p. 397
B. csikii	+	—	—	—			—	—		—	—	
B. harpalinus	+	+	+	—	+	—			—	—	—	
B. ponderosus	—	—	—	—	—	+	—	—	—	—	?	
B. similis	+	?	+	+	+		—	—	—	—	—	
B. verbasci	+	—	—	—	—		—		—	—	—	
Broscus cephalotes	+	?	?	?	+	—	—			—	—	
Calathus ambiguus	+	+	+	+	+	—	—	—	—	—	—	
C. erratus	+	?	+	+	+	?	—	?	—	—	—	To Finland, also from Sweden
C. fuscipes	+	—	+	—	+		—	?	—	—	—	
C. melanocephalus	+	?	+	+	+	+	+	+	+	+	+	
C. micropterus	+	—	+	?	+	+	?	+	+	+	?	
C. mollis	+	+	+	—	—	—	—	—		—	—	
C. piceus	+	—	—	—	—	—	—	—	—	—	—	
Calosoma auropunctatum	+	?	?	—	—	—	—	—	—	—	—	
C. denticolle	—	—	—	+	—	—	—	—	—	—	—	
C. inquisitor	+	?	—	+	—	—	—	—	—	—	—	
C. investigator	—	—	+	—	—	—	—	—	—	—	—	
C. reticulatum	?	—	+	—	—	—	—	—		—	—	
C. sycophanta	+	—	—	—	—	—	—	—	—	—	—	
Carabus arvensis	+	?	—	—	+	—	—	—	—	—	—	
C. auratus	—	+	—	—	—	—	—	—	—	—	—	Anthropochorous
C. cancellatus	+	?	—	+	+		—	—	—	—	—	To northern Sweden partly across the Bothnian Sea.
C. clathratus	+	?	+	+	+	+	—	?	—	—	?	
C. convexus	+	?	—	+	+	—	—	—	—	—	—	

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Carabus coriaceus	+	?	—	—	—	—	—	+	—	—	—	
C. glabratus	+	—	?	?	+	+	+	+	+	+	?	
C. granulatus	+	?	+	+	+	+	—	?	—	—	—	
C. hortensis	+	+	?	?	+	—	—	?	?	—	—	
C. intricatus	+	—	—	—	—	—	—	—	—	—	—	
C. menetriesi	—	—	—	—	+	—	—	—	—	—	—	
C. monilis	—	+	?	—	—	—	—	—	—	—	—	Probably anthropochorous
C. nemoralis	+	?	—	?	+	—	—	—	—	—	—	
C. nitens	+	?	+	?	+	+	?	?	+	?	?	p. 744
C. problematicus	+	?	—	?	—	—	?	+	+	+	?	p. 744
C. violaceus	+	?	+	+	+	+	—	+	+	—	—	p. 742
Chlaenius costulatus	—	—	—	?	+	?	—	—	—	—		
C. nigricornis	+	—	+	+	+	—	—	—	—	—	—	
C. quadrisulcatus	+	—	?	—	+	—	—	—	—	—	—	
C. sulcicollis	+	—	?	+	—	—	—	—	—	—	—	
C. tristis	+	?	+	+	+	—	—	—	—	—	—	
C. vestitus	+	—	—	—	—	—	—	—	—	—	—	
Cicindela campestris	+	?	+	?	+	?	—	?	?	—	—	
C. hybrida	+	?	—	—	+	—	—	—	—	—	—	
C. maritima	+	—	—	+	+	+	—	+	?	+	?	
C. silvatica	+	?	+	+	+	+	—	—	—	—	—	
Clivina collaris	—	—	—	—	—	—	—	—	—	—	—	Anthropochorous
C. fossor	+	?	+	+	+	+	?	+	+	+	?	
Cyhrus caraboides	+	—	+	+	+	+	+	+	+	+	?	
Cymindis angularis	+	?	+	+	+	—	—	—	—	—	—	
C. humeralis	+	—	+	—	—	—	—	—	—	—	—	
C. macularis	+	+	+	?	+	?	—	—	—	—	—	
C. vaporariorum	+	—	?	?	+	+	?	+	+	+	?	
Demetrias imperialis	?	—	+	—	—	—	—	—	—	—	—	
D. monostigma	+	—	+	?	—	—	—	—	—	—	—	
Diachila arctica	—	—	—	—	—	—	?	—	—	+	?	
D. polita	—	—	—	—	—	—	+	—	—	—	?	
Dichirotrichus pubescens	+	?	?	—	—	—	—	?	+	+	+	p. 751
D. rufithorax	—	—	—	+	+	—	—	—	—	—	—	
Dolichus halensis	+	—	—	—	—	—	—	—	—	—	—	
Dromius agilis	+	?	+	?	+	?	—	?	?	—	—	

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Dromius angustus	+	+	+	—	—	—	—	—			—	
D. fenestratus	+	?	+	+	+	—	—	—		—		
D. linearis	+	—	+	?	+	—	—	—		—	—	
D. longiceps	+	—	—	?	?		—	—		—	—	
D. marginellus	+	?	?	?	+	—	—	—	—		—	
D. melanocephalus	+	—	—	—	—	—	—	—	—	—	—	
D. nigriventris	+	?	+	—	—	—	—	—	—	—	—	To Finland from Sweden
D. quadraticollis	—	—	—	+	—	—	—	—	—	—	—	
D. quadrimaculatus	+	?	?	—	—	—	—	—	—		—	To Finland from Sweden
D. quadrinotatus	+	?	+	?	—	—			—	—		
D. sigma	+	—	+	?	+	+	—	—	—	—	—	
Dyschirius aeneus	+	—	+	?	+	—	—		—	—	—	
D. angustatus	+	—		—	?	+		+	+	?	—	p. 743
D. chalceus	+	—	—	—	—	—	—			—	—	
D. globosus	+	?	+	+	+	+	—	+	+	+	?	
D. helléni	—	—	—	—	—	+	—	+	+	?	?	p. 742
D. impunctipennis	+	+	+	?	+	—	—	—	—	—	—	
D. intermedius	+	—	—	—	+	—	—	—	—	—	—	
D. lüdersi	+	?	+	+	+	+			—	—	?	
D. neresheimeri	—	—	—	?	—	—	—	—	—	—	—	
D. nitidus	—	—	—		+			—	—	—	—	
D. obscurus	+	+	+	+	+	?				—	—	
D. politus	+	+	+	?	+	?				—	?	
D. "rufipes"	—	—	—	—	+	—				—	—	
D. salinus	+	—	+	+	—	—	—	—	—	—	—	
D. septentrionum	—	—	—		+	+		+	+	+	—	p. 749
D. thoracicus	+	+	+	+	+	—	—	—	—	—	?	
Elaphrus angusticollis	—	—	—	—	+			—	—		—	
E. cupreus	+	?	+	+	+	?	—	+	+	+	?	
E. lapponicus	—	—	—	—		?	—	+	+	?	—	p. 741
E. riparius	+	?	+	+	+	?	?	+	+	+	?	
E. uliginosus	+	?	+	?	+	?		?	?	—	—	
Harpalus aeneus	+	?	+	+	+	?		—	—	—	—	
H. anxius	+	—	+	—	+	—		—	—		—	
H. asureus	—	—	+	—	—	—	—	—	—	—	—	
H. calceatus	+	?	+	+	+				—	—	—	
H. distinguendus	+	?	—	—	+	—	—	—	—	—	—	

	Southern immigration			Eastern immigration				Wurm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Harpalus frölichi	+	—	?	—	—	—	—	—	—	—	—	
H. fuliginosus	+	?	—	—	+	+	?	?	—	—	?	
H. griseus	+	+	+	—	+	—	—	—	—		—	
H. hirtipes	+	—	+	—	—	—	—	—	—	—	—	
H. latus	+	?	+	+	+	+	?	?	?	—	—	
H. luteicornis	?	?	+	+	+	—	—	—	—	—	—	
H. melancholicus	+	—	+	—	—	—	—	—	—	—		
H. melleti	+	—	+	—	—	—	—	—	—	—	—	
H. neglectus	+	—	?	—	—	—	—	—	—	—	—	
H. nigritarsis	—	—	—	—	—	?	—	—	—	?	?	
H. picipennis	+	—	+	—	—	—	—	—	—	—	—	
H. pubescens	+	?	+	+	+	—	—	—	—	—	—	
H. punctatulus	—	—	+	+	+	—	—	—	—	—	—	
H. puncticeps	+	—	?	—	+	—	—	—	—	—	—	
H. puncticollis	+	?	?	—	+	—	—	—	—	—	—	
H. quadripunctatus	+	?	+	?	+	+	—	+	+	?	—	
H. rubripes	+	?	+	?	+	—	—	—	—	—	—	
H. rufitarsis	+	—	?	—	—	—	—	—	—	—	—	
H. rufus	+	—	?	—	—		—		—	—	—	Perhaps introduced into Ab Åbo
H. rupicola	—	—	+	—	—	—	—	—	—	—	—	
H. seladon	+	?	+	+	+	—	—	—	—	—	—	
H. serripes	+	—	+	—	—	—	—	—	—	—	—	
H. servus	+		?	—	—	—	—		—	—	—	
H. smaragdinus	+	?	+	?	+	—	—	—	—	—	—	
H. tardus	+	?	+	+	+	?	—		—	—	—	
H. vernalis	+	—	+		—	—	—	—	—	—	—	
H. winkleri	+		—	—	+	—	?	?	+	?	—	p. 747
Lebia chlorocephala	+	—	+	+	+	—	—		—	—	—	
L. crux-minor	+		+	+	+	—	—	—	—	—	—	
L. cyanocephala	+	?	+	?	+	—		—	—	—	—	
Leistus ferrugineus	+	?	+	?	+	—		+	+	—		p. 747
L. rufescens	+	?	—	?	+	—	—	+	+	—	—	
L. rufomarginatus	+	—	—	—	—	—		—		—	—	
Licinus depressus	+	—	+	—	—	—	—	—	—	—	—	
Lionychus quadrillum	—	—	—	—	—	—	—	—	—	—	—	Probably displaced to Sweden
Loricera pilicornis	+	?	+	+	+	?	—	+	+	?	?	
Masoreus wetterhalli	+	—	+	—	—	—	—	—	—	—	—	

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Metabletus foveatus	+	—	+	—	+	—	—	—	—	—	—	To Finland also from Sweden
M. truncatellus	+	?	+	+	+	?	—	—	—	—	—	
Microlestes maurus	+	—	+	—	+	—	—	—	—	—	—	
M. minutulus	+	—	+	+	+	—	—	—	—	—	—	
Miscodera arctica	+	—	+	?	+	?	?	+	+	+	?	p. 756
Nebria brevicollis	+	?	+	—	—		—	?	—		—	
N. gyllenhali	?	?	+	?	+	+	+	+	+	+	?	p. 742
N. gyll. balbii	—	—	—	—	—	—	?	—	+	?		p. 742
N. livida	+	+	+	—	+	—	—	—	—	—	—	
N. nivalis	—	—	—	—	—	—	+	+	+	+		p. 763
N. salina	+	?	+	—	—	—	—	?	—	—	—	
Notiophilus aquaticus	+	+	+	+	+	+	+	+	+	+	+	p. 409
N. biguttatus	+	+	+	+	+	?	—	+	+	?	—	p. 405
N. germinyi	+	?	+	?	+	?	?	+	+	+	?	
N. palustris	+	?	+	+	+	+	—	?	—	—	—	
N. pusillus	+	+	+	+	+	—	—	—	—	—	—	
N. reitteri	—	—	—	—	?	+	?	—	?	+	?	
N. rufipes	+	—	—	—	—	—	—	—	—	—	—	
Odacantha melanura	+	—	+	?	+	—	—	—	—	—	—	
Olisthopus rotundatus	+	?	+	+	+	—	—	?	—	—	—	
Omophron limbatum	+	—	—	—	—	—	—	—	—	—	—	
Oodes gracilis	?	—	—	—	—	—	—	—	—	—	—	
O. helopioides	+	—	+	+	+	—	—	—	—	—	—	
Panagaeus bipustulatus	+	—	+	?	+	—	—	—	—	—	—	
P. crux-major	+	—	+	+	+	—	—	—	—	—	—	
Patrobus assimilis	+	?	+	—	+	+	+	+	+	+	?	
P. atrorufus	+	?	+	?	+	—	—	+	+	—	—	p. 747
P. septentrionis	—	—	—	—	?	+	+	+	+	+	?	p. 744
P. sept. australis			—	—	+	—	—	—	—	—	—	
Pelophila borealis	—	—	—	—	+	+	+	+	+	+	?	
Perileptus areolatus	?	—	—	—	+	—	—	?	—	—	—	
Pogonus luridipennis	—	+	—	—	—	—	—	—	—	—	—	
Pristonychus terricola	—	—	—	—	—	—	—	—	—	—	—	Anthropochorous

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Pterostichus adstrictus	?	—	—	—	?	?	—	+	+	+	?	p. 744
P. aethiops	—	—	—	?	+	—	—	—	—	—	—	
P. angustatus	+	+	—	?	+	—	—	—	—	—	—	
P. anthracinus	+	—	+	—	+	—	—	—	—	—	—	
P. aterrimus	+	+	+	+	+	—	—	—	—	—	—	
P. coerulescens	+	?	+	+	+	?	—	—	—	—	—	
P. cupreus	+	?	+	+	+	—	—	—	—	—	—	
P. diligens	+	?	+	+	+	+	—	+	+	+	?	
P. fastidiosus	—	—	—	—	—	—	+	—	—	—	—	
P. gracilis	+	—	+	+	+	—	—	—	—	—	—	
P. lepidus	+	?	+	?	+	+	—	?	—	—	?	Certainly displaced to Finland
P. madidus	—	—	—	—	—	—	—	—	—	—	—	
P. middendorffi	—	—	—	—	—	—	+	—	—	—	—	
P. minor	+	?	+	+	+	+	—	?	—	—	+	
P. niger	+	?	+	?	+	—	—	+	+	—	—	
P. nigrita	+	?	+	+	+	+	—	+	+	—	—	
P. oblongopunctatus	+	?	+	+	+	?	—	+	+	—	—	
P. punctulatus	+	—	—	—	—	—	—	—	—	—	—	
P. strenus	+	—	+	+	+	+	—	+	+	—	+	p. 395
P. vernalis	+	?	+	+	+	—	—	—	—	—	—	
P. vulgaris	+	?	+	?	+	—	—	—	—	—	—	
Sphodrus leucophthalmus	—	—	—	—	—	—	—	—	—	—	—	Anthropochorous
Stenolophus mixtus	+	—	?	?	+	—	—	—	—	—	—	
S. teutonus	+	—	—	—	—	—	—	—	—	—	—	
Stomis pumicatus	+	—	+	—	+	—	—	—	—	—	—	
Synuchus nivalis	+	?	+	?	+	—	—	?	—	—	—	
Tachys bistriatus	—	—	—	—	+	—	—	—	—	—	—	
T. bisulcatus	?	—	—	—	+	—	—	—	—	—	—	
Tachyta nana	?	—	—	—	+	?	—	—	—	—	—	
Trachypachys zetterstedti	—	—	—	—	+	—	—	—	+	—	—	
Trechus discus	+	—	—	?	+	—	—	—	—	—	—	
T. fulvus	—	—	—	—	—	—	—	+	—	—	—	p. 791
T. micros	+	—	—	?	+	—	—	—	—	—	—	
T. obtusus	+	—	+	—	—	—	—	+	+	—	—	p. 762
T. quadristriatus	+	?	+	+	+	—	—	—	—	—	—	

	Southern immigration			Eastern immigration				Würm hibernation				Remarks
	Through Skåne	Through Skagerrak	Directly to Öld-Gtl	Across the Gulf of Finland	Between Gulf of Finland and White Sea	Through Kuusamo-Salla	Through Kanin-Kola	In southwestern Norway (south of latitude 64°N)	In northwestern Norway (eastward as far as Nordkapp)	In the northeast (Veranger-Petsamo)	On the White Sea	
Trechus rivularis	+	—	—	+	+	—	—	—	·	—	—	
T. rubens	+	?	?	+	+	?	—	+	+	—	—	
T. secalis	+	-	+	?	+	—	—	+	?	—	—	
Trichocellus cognatus	+	?	+	+	+	+	?	+	+	+	?	p. 742
T. mannerheimi	—	—	+	—	—	—	+	—	—	—	—	
T. placidus	+	?	+	+	+	-	—	+	+	—	—	
Zabrus tenebrioides	+	—	—	—	—	—	—	—	—	—	—	
Total*	265 (+16) = 281	26 (+114) = 140	183 (+43) = 226	130 (+73) = 203	231 (+9) = 240	72 (+45) = 117	22 (+25) = 47	72 (+34) = 106	79 (+16) = 95	45 (+20) = 65	11 (+55) = 66	
	280 (+ 12) = 292 (81,6%)			267 (+ 23) = 290 (81,0%)				97 (+ 33) = 130 (36,3%)				

*In the sum and percentage calculation, 7 anthropochores are excluded (*Carabus auratus, C. monilis, Clivina collaris, Lionychus, Pristonychus, Pterostichus madidus, Sphodrus*), whereas three subspecies (*Badister bipustulatus lacertosus, Nebria gyllenhali balbii, Patrobus septentrionis australis*) are considered as separate entities.

An example of how the multiple origin of a more or less pan-Fennoscandian species can be envisaged is provided by the "clarified" map of *Bembidion saxatile* (Fig. 116).

The varied postglacial history of most of the species is easily understandable. Strictly speaking, there is no question of a new colonization. We are dealing with the interglacial fauna, which was pushed to all sides by the ice and is now moving back into the old region.

The influence of the last glaciation on the fauna and flora of Fennoscandia may be simply expressed as follows: This period had a decisive role for the present-day local distribution of every species. But the stock of Fennoscandian species was little changed.

English Summary*

813 The two first parts of this book, published in 1945, contain a full account of the distribution, ecology, "biology" and dynamics (i. e. power of dispersal) of every species of the *Carabidæ,* 361 in number, occurring in Fennoscandia. Distribution maps (part II) are given for nearly all of them.

The present IIIrd part of the work deals with the material from general points of view with the chief purpose of elucidating the glacial and postglacial history of the Fennoscandian fauna.

p. 7. Preface. The necessity of carrying out experiments for solving problems within the domain of ecological zoogeography is maintained.

p. 10. Introduction to the IIIrd part. This investigation is no complete survey of all ecological and zoogeographical questions regarding the Fennoscandian Carabidae. Above all the synecology was almost completely neglected for reasons given on p. 35 a. f. Any attempt to make a zoogeographical division of the area† treated on the basis of the Carabidae was also abandoned. The species populations in different parts of Fennoscandia seem unusually stable and there are but few examples of clear subspecies; thus — with the exception of the state of the flying-wings (p. 335 a. f.) — no investigation of the variability of each species within the area was realized.

The word postglacial was used mainly in a biological sense and thus includes the late glacial time (acc. to the geologists). — For the term "Ausbreitungsökologie", created by Ekman (1922), in this book — also in the Ist part — "Dynamik" was consequently used. In accordance with this "ausbreitungsökologische" and "existenzökologische" limits of the area of a species are called dynamic limits and existence limits respectively.

p. 13. On modern insect taxonomy. Its three main features are: the splitting up of genera; the alteration of the names of species; the breaking up of species into smaller categories.

Experts are recommended to proceed with the greatest caution in dividing up wellknown genera into smaller ones. The postulated new units usually had better be treated as subgenera or species-groups. The genera — "for practical reasons" (in the widest sense of this expression) — should be too large rather than too small.

It is of special importance that a specific name is never transferred from one species to another. In actual cases — in spite of the rules of priority — it is better to let the name in question lapse. The consequences of the priority-rules strictly applied, on the whole, are many unnecessary confusions, especially when old names, long forgotten, are dug out from the literature, "interpreted" and used to replace universally prevailing names. It would be worth while to consider regarding specific names given before, say, 1850 and not (or merely as synonyms) scientificially used after, say, 1900 as invalid in favour of later used names.

p. 26. On the consideration of the literature. The zoological — and particularly the entomological — publications during the present century have increased in number and size to such an extent that a complete mastery of its results, even within a restricted branch, is hardly possible. In "border-sciences", such as zoogeography, these difficulties are especially severe. The zoogeographer

*Reproduced from the German original, pp. 813–842—General Editor.

†(= "region" throughout the translation; cf. p. 822; suppl. scient. edit.).

814 must know, however, as completely as is possible all the literature concerning the animals constituting his special subject, in order to get fully acquainted with their taxonomy, distribution, ecology etc. He thus produces the foundation for general conclusions. Thereby he comes into contact with several auxiliary sciences, with botany, general geography, geology, climatology etc. in which he usually is but a layman. It therefore seems reasonable that the zoogeographer attacks his problems concerning the history of each species, mainly on the ground of his special knowledge, i. e. proceeding from the animal studied, and thus that he must not feel himself *too* much bound by the auxiliary disciplines. His literature studies consequently can be reduced to moderate proportions. Thus a complete knowledge of the *case* treated is more important than that of the *methods* used by other investigators on other subjects.

p. 29. *On the task of the museums.* On the basis of 10 questions sent to the curators of the large museums of Fennoscandia and Denmark the present status of the coleopterous collections of each of their own countries and the rules for their organization was put together. Some desiderata for the future were suggested which could be summarized as follows:

All exactly labelled material is valuable. "Duplicates" do not exist. It is necessary to strive after long series of specimens collected together in order to know the variability of the population. This means a considerable increase of work on the part of the museum's personnel, a problem which could be solved, however, if their efforts on the whole were more concentrated upon the investigation of *the fauna of their own country* and the common ambition to establish a palaearctic or even a world collection was correspondingly reduced. The most practical measure would be to divide the home collection into a concentrated "type collection" (with say 2 ♂ and 2 ♀ per species, excellently mounted) for rough taxonomical purposes on the one hand, and a large "elastic" geographical main collection on the other. Special collections, such as those quoted in monographical publications, from islands or other restricted territories, from certain habitats etc., should not be too much avoided but it is recommended to put with the respective species in the main collection a reference in the form of a label to such separated material.

p. 35. *On synecology and "syngeographie".* I take an extremely sceptical attitude to all sorts of collective treatment of animal species as members of an ecological "community" or of a zoogeographical "region". Especially in terrestrial animals which are non-sedentary the "struggle for space" must play an unimportant rôle. Further I am unable to believe that the organic nutriment produced by the green plants as a rule is fully exploited by the "consumers" or even that there exists an exact limit up to which this nutriment may be consumed without disturbing the "equilibrium of nature". In my opinion the terrestrial "zoocoenoses" are as a rule non-saturated. The idea of FRIEDERICHS and THIENEMANN of zoocoenoses as something like an organism seems to me quite out of touch with realities.

Under all circumstances it must be worthless to create "zoocoenoses" founded on Carabids alone as these constitute merely a fragment of the consumer group and thus cannot be expected to behave as a constant.

It is impossible to maintain, however, that synecology *must* be a biological branch working with constructions only, lying beyond the reach of exact results

815 But the condition precedent is a sufficient knowledge of the autecology of each species constituting the biocoenosis.

p. 43. The uniting of organisms into groups with ± corresponding distribution or the creating of "regions", each with its characteristic animals and plants, may be termed "syngeography". The regional division of greater or smaller parts of the earth becomes quite different according to the animal or plant group used as a starting point. On the other hand it is easy to observe that the proposed animal regions e. g. of Fennoscandia (EKMAN 1922) agree in all important features very well with the botanical, i. e. the forest regions. I have found no reason to propose a new regional system on the basis of Carabidae but feel it satisfactory enough simply to take over the forest regions of the Fennoscandian botanists (fig. 61).

Analytic part.

p. 48. Experiment journal. The purpose of the experiments made was to isolate such external factors affecting the animals in nature as temperature, moisture and light, and to study the reactions of the animal to them. Above all the preferenda were investigated by means of different sorts of "orgels". In many cases also the resistance against extreme temperatures and desiccation was studied. It is of special importance to point out that the figures obtained are not absolute, partly because of uncontrolled factors influencing the experiment, partly owing to the fact that one and the same species — even the same individual in different situations — often shows different reactions. Consequently I tried to avoid these difficulties by making the same experiment — simultaneously or in the nearest possible identical circumstances — with more than one species. Thus it was possible to obtain at least comparative figures, e. g. for the temperature preferenda of a series of taxonomically and ecologically closely related species, which proved sufficient for the tasks selected.

The following experiments are of general importance: — 1. 15 spec. of the clearly eurytopic *Pterostichus nigrita* were individually marked and examined during the 10 following experiments in the temperature "orgel" apparatus. Only the consecutive order of the individuals in the apparatus was noted. Their distribution proved to be regulated by chance only (Diagr. 2). The eurythermous character of this species thus seems to be founded, not on the presence of several biotypes (ecotypes) within the species, but simply on the relative insensibility of each individual. — 2. The question of stable and labile preferenda, briefly treated in an earlier paper (LINDROTH 1943 a), was attacked on other species. *Pterostichus anthracinus, Harpalus serripes* and *Brachynus crepitans* have a stable, *Harpalus punctatulus* a pronouncedly labile temperature preferendum. In the last-mentioned case the instability of the reaction to humidity seems to be decisive. — 3. *Brachynus crepitans* and *Agonum dorsale* regularly occur together without having any dependence on each other. They represent the rare case of two species with nearly identical ecological demands. It might thus be expected that a comparison between the reactions of these two species in current preferenda and resistance experiments would reveal those of the greatest ecological importance, i. e. those in which they behave in the same manner. This proved to be the case, regarding temperature as to cold-resistance, regarding moisture as to the preferendum. It ought to be justifiable to regard the experimental results on these two ranges as especially important for ± xerophilous Carabids.

816 All the experimental results, with two exceptions (Diagr. 11, 46), were treated by simple arithmetical methods. Above all it is necessary to point out that the distribution of individuals in the temperature "orgel" is not regulated by chance only as the hot zone of the apparatus constitutes a complete barrier, without an equivalent at the cold end. Therefore the common use of statistical methods on these figures gives no advantage. In pronouced hygrophilous species the average temperature preferendum, however it may be calculated, is much too low.

The simple apparatuses used in the different experiments appear from fig. 3—8. A new construction is the so called "universal orgel" in which the animals were exposed to the simultaneous influence of 2—3 factors (temperature, moisture, light). The corresponding diagrams are seen on p. 141 a. f.

In the journal (p. 69—111), to which reference is made from every experiment treated in the text, complete data are given for each separate experiment.

p. 112. The "limestone-species". It is a well-known fact that many plants are dependent on limestone. Also several insects, among these some Carabids, are usually termed calciphilous, in Fennoscandia above all species characteristic of the islands of Öland and Gotland, partly occurring also within the isolated cambro-silurean districts of central S-Sweden or SE-Norway (fig. 9, 10). The genus *Harpalus* is especially rich on such species, including the only three found in Scandinavia exclusively on Öland and Gotland. So a series of 15 *Harpalus* species was selected for closer experimental investigation.

p. 119. The Harpali are clearly polyphagous and their, in many cases very restricted, geographical distribution — above all in limestone districts — cannot be due to specialized food-habits.

p. 120. In the substratum-"orgel" all species tested seemed insensible to different admixture of $CaCO_3$, even if dissolved in water saturated with CO_2 (tab. 2, 3).

p. 124. No more the species in question seem to react to the degree of pH of the substratum (tab. 4).

p. 125. A series of experiments was made in order to show whether the suggested "calciphilous" Carabids are able to distinguish between gravel from lime-stone and from siliceous rocks (tab. 5). Actually, 5 species of *Harpalus* (in addition *Panagaeus bipustulatus)* seemed to prefer the firstnamed sort.

p. 127. With these 6 species the experiments were repeated, but after substituting the siliceous gravel by clay-schist gravel, free from $CaCO_3$ but as regards other qualities practically indentical with the limestone (tab. 6). None of the species showed preference for the latter sort in this case.

p. 128. The experiments accordingly seemed to prove that an eventual confinement to limestone, shown by the Carabids investigated must be due to demands other than chemical. So their reactions to thermal and hygric factors were tested in the usual manner (diagr. 19—24). A summing-up given in tab. 7 (p. 137) shows that the supposed "calciphilous" Harpali are to a great degree either thermophilous or xerophilous insects, or both.

p. 139. An attempt to decide what factor in each species plays the most important rôle was made through experiments in the "universal orgel" (vide p. 85) where especially the strength of reactions to the simultaneous influence of thermal and hygric factors was studied (diagr. 25—35). Among the 11 *Harpalus* species tested *azureus* (p. 174) proved to have the greatest demands for warmth, *serripes* for

817 dryness. Contrary behaviour is shown by *aeneus,* the most ubiquitous species, the thermal preferendum of which not only lies low but is also easily disturbed by the influence of other factors. This may be the criterion of every eurytopic and widely-distributed species.

p. 176. *Harpalus Melleti* and *rupicola* are peculiar, not xerophilous and but slightly thermophilous. Evidently, the restricted distribution of these species is due to demands which cannot be elucidated by means of preferenda experiments. The cold-resistance (diagr. 20) — determinating the length of the annual period of activity — seems in these cases more important.

p. 177. The thermal qualities of the rock and gravel of cambro-silurean limestone compared with those of granite were first studied by means of laboratory measurements on small quantities (diagr. 36—39). All reactions proved to be more rapid in granite which therefore had the highest daily maxima and the lowest minima.

p. 181. To a more pronounced degree the same differences were observed in field measurements on each side of a fault fissure (cambro-silurean limestone *contra* granite) at Dlr Rättvik, Sjurberg (fig. 14—16, diagr. 40). It seems justifiable to say that the cambro-silurean limestone — as regards temperature — alters the microclimate in an oceanic direction. The comparatively high minima no doubt have a great biological influence.

p. 187. The higher evaporation effect of limestone gravel was demonstrated by a simple experiment (diagr. 41).

p. 188. The principle biological advantage created by the cambro-silurean limestone no doubt is the lengthening of the annual period of activity. With the summer-temperature during a period of 20 years at Visby on the isle of Gotland as a starting-point, an attempt was made to estimate this prolongation (diagr. 42, tab. 8). One comes to an average value of three weeks.

p. 192. A hypothetical map of southern Sweden was drawn, in order to illustrate the positive thermal influence of limestone on minimum temperature in May and September (fig. 17). This map, however, is valid only for thin soil-layers resting on firm rock.

p. 193. Archaic limestone, e. g. marble, or limestone ocurring as moraine only, both widely distributed in central Sweden, seem not to cause any positive biological effect on the ground-fauna, as, no doubt, would have been the case if the influence had been of a chemical character. One feels inclined, therefore, to regard the "petrophilous" insects, especially treated by Holdhaus for the Alps, as controlled by thermal and hygric rather than by chemical factors.

p. 196. The autotrophic plants are no doubt in many cases dependant on direct or indirect chemical qualities of $CaCO_3$. It seems evident, however, that botanists at present show a tendency to underestimate the thermic and hygric importance of limestone.

p. 198. The fauna of the islands. The Carabid fauna of 21 Fennoscandian island-districts (fig. 18, tab. 9), each with one or two comparison areas on the mainland, was analysed. The species were arranged according to dynamic groups (tab. 10—12), hibernation types (tab. 13) and ecological groups (tab. 14).

p. 235. 1. Hailuoto (Karlö) is the youngest island treated (maximum age 2000 years) but, nevertheless, has quite a "normal" fauna, no doubt due to its situation — extraordinarily favourable for hydrochorous dispersal — right at the mouth of a large river.

818 p. 236. 2. Åland (mainland). According to A. PALMGEN the flora of Åland has immigrated to the island mainly from the west, from Sweden. The composition of its Coleopterous fauna suggests that the path from the east, from Balticum and the mainland of Finland, has played an at least equally important rôle.

p. 241. The "western" group of Åland-Coleoptera contains many flightless species and forms, the "eastern" one — with few exceptions — only species capable of flight. The flora shows no similar division and the direction of prevailing winds (fig. 20) gives no explanation.

p. 256. The indisputable fact — documented also in other parts of the area (p. 291, 593) — that an anemochorous dispersal of insects in the Baltic area has taken place more from the east toward the west than in the opposite direction, was studied by means of experiments in a flight-direction apparatus (fig. 8, p. 109). It appeared that at least some Carabids, swarming as a rule in the evening, show a tendency to start their flight towards the sun, i. e. in the main towards the west (fig. 21, tab. 19).

p. 258. The immigration of flightless beetles from Sweden to Åland may have taken place by means of ice-drift in the spring.

p. 260. 3. The "skärgård" of SW Finland (excl. Åland). In this archipelago the ice- and waterdrift seems to have been of still greater importance (cf. fig. 22).

p. 263. 4. Hogland and 5. the other "Outer Isles" in the Gulf of Finland. In accordance with its considerably greater age Hogland possesses a higher percentage of flightless Carabids than the other "Outer Isles", the youngest of which, Seiskari, shows a higher figure of macropterous species and forms than any other Fennoscandian island.

p. 273. 6. Valamo (in Ladoga). The fresh water may have facilitated a hydrochorous transport.

p. 274. 7. Värmdön. In accordance with the position close to the mainland the fauna is completely "normal".

p. 276. 8. Ösel and Dagö. The natural conditions (incl. the flora) agree in many respects with those of Gotland and Öland. The Carabid faunas are more different.

p. 279. 9. Gotska Sandön. This is a standard example of a young and highly isolated island having got its fauna totally by means of over-sea-immigration. The percentage of flightless species and forms, in keeping with this, is extremely low. The famous insect species known in N Europa exclusively from Gotska Sandön are all capable of flight. The fauna has no doubt invaded the island by means of anemochorous(incl. anemohydrochorous) transport, of which concrete observations have been made. Introduction by man seems to have been of minor importance.

p. 285. 10. Fårön. The vicinity of the mainland of Gotland has given the fauna a more "normal" stamp but a direct invasion, mainly by air, from the east has given remarkable additions.

p. 289 a. f. 11—13. The large Baltic isles, Gotland, Öland and Bornholm, are at first briefly described separately and then (p. 298 a. f.) the common problems (also for Ösel — Dagö) concerning the origin of their fauna and flora are discussed. It is striking that the relationship of the Öland—Gotland flora —

819 in accordance with the similar geology — points to Ösel—Dagö whilst the coleopterous fauna points to the south (tab. 23, fig. 23).

p. 303. A list of Coleoptera known in Sweden only from Öland and Gotland contains 14 species common to both isles, 5 of which are flightless; among the remaining 46 species only 2 are incapable of flight. Taking the whole Carabid fauna under consideration we find likewise that species common to Öland and Gotland — and also to Bornholm — are characterized in general by a restricted power of dispersal. It is difficult to understand these facts without the assumption of a postglacial, ± direct land connection between the islands in question.

p. 308. For geological reasons such a connection between Öland—Gotland and the present south coast of the Baltic can hardly have existed later than during the early Ancylus Period. Pollenanalytical investigations of recent years have proved, however, that the flora already contained many heatrequiring forms at that time.

p. 310. Examples of equivalent Carabids are *Harpalus azureus* and *Calathus mollis*.

p. 312. 14. Ven. The most characteristic feature of this island is the radical influence of cultivation. Several Carabid species have no doubt been introduced by man.

p. 314. 15. The "skärgård" off Göteborg. The percentage of brachypterous species and forms among Carabids is remarkably high. This seems, however, to a great extent to be due to anthropochorous transport.

p. 315. 16. Orust and 17. Hvaler show nearly "normal" faunas.

p. 318. 18. Hitra (and adjacent islands). This district is characterized by an exceptionally high percentage of functionally brachypterous Carabids. This fact is not due to any extraordinary influence of selection but to the former existence of a glacial refuge in the immediate vicinity.

p. 321. 19. Dönna (and adjacent isles) and 20. Lofoten (and Vesterålen) show the same feature to a somewhat slighter degree. It is significant, however, that in the outer isles (Væröy, Röst) the brachypterous element is most dominant. Among the islands in Troms and Finnmark (p. 324) this holds good for Nordfuglöy. This case is especially interesting as it forms a clear proof that the brachypterous element has not been introduced by man.

p. 325. An analysis of some other islands of Western Europe (tab. 25) has shown that the isolated and exposed position of an island (e. g. Helgoland) does not in itself cause a selection in favour of brachypterous species and forms, at any rate not within the comparatively short postglacial time.

p. 331. A summary of conclusion made on the basis of the island-faunas studied makes it i. a. clear that on moderately isolated islands the immigration of flying insects is rather more favoured than on the continent, whereas, of course, flightless forms are greatly disfavoured.

p. 334. Wing dimorphism. In the fam. *Carabidae* the wing dimorphism is of the asexual type. In Fennoscandia 50 species (out of 362) occur in both forms (tab. 27); 18 other species have proved to be dimorphic in other parts of their range. Some species are rather polymorphic but all forms with not fully developed flying wings are here termed brachypterous.

p. 343. The wing dimorphism of Coleoptera as a whole seems to have a here-

820 ditary basis. This has been proved for *Sitona hispidulus* (JACKSON 1928) and *Pterostichus anthracinus.* Brachypterous wing is a dominant and the macropterous individuals, consequently, are homozygotes which cannot give brachypterous offspring, unless by means of recurrent mutation.

p. 347. In several constantly brachypterous species of Coleoptera — likewise in brachypterous individuals of dimorphic species — the reduction of flying wings may be correlated with other morphological changes. Of these the following are represented among the dimorphic Carabids investigated:

a) Reduction of flight muscles. This is remarkable also in a macropterous specimen of *Pterostichus vulgaris* (Dlr Lima) with completely reduced muscles.

b) Reduction of metathorax. In *Calathus melanocephalus* there seems to be no difference in this respect between the two forms but brachypterous *C. mollis* is on the other hand almost constantly characterized by its shorter metepisterna.

c) Fastening of elytra along the suture. A real ancylosis seems not to occur among dimorphic Carabids but a suggestion of it is visible in single (as a rule brachypterous) specimens of *Calathus erratus* and *Pterostichus lepidus.*

p. 351. A case of preserved psychical (and partly muscular) functions ordinarily connected with flight in a brachypterous specimen of *Bradycellus collaris* is described.

p. 351. None of the morphological changes commonly correlated with reduction of flying wings seems to be constant. It is therefore probable that they are due to special genes.

p. 352. The influence of selection. The best study on the biological importance of flight to Coleoptera (espec. Carabids) is that of DARLINGTON (1943). He suggests a selection in favour of flightless forms in mountain districts as well as on most islands (exceptions are flat, tropical and young islands). According to him the brachypterous individuals, forms and species are favoured owing to their general higher "viability" which he finds proved among other things by the breeding experiments made by JACKSON on *Sitona hispidulus.* — A series of experiments on preference and resistance, simultaneously with brachypterous and macropterous individuals of the same species, was made (diagr. 43—46). No general "higher viability" of the brachypterous form appeared. Therefore, although the material used was rather small, it hardly seems justifiable to ascribe *a priori* a higher selection value to the brachypterous form of a dimorphic Carabid species.

p. 360. The actual distribution of the two forms in Scandinavia, e. g. in *Notiophilus biguttatus,* seems likewise to contradict the idea of a general superiority of the *f. brachyptera.*

p. 361. The selective importance of flight power† itself was already maintained by DARWIN, especially in the case of Madeira. DARLINGTON, on the other hand, stresses the opinion that for species living on islands or in mountains the power of flight must be regarded as "useless but not necessarily harmful", i. e. that this function in itself has no negative selective effect. He seems to base this view on the fact that flightless Carabids are evidently favoured not only in barren wind-exposed but likewise in densely wooded mountains. Also to my mind the wind exposure was overestimated by DARWIN

†(="flight capacity" throughout the translation in accordance with Thiele, H. (1977): Carabid beetles in their environments. Springer, New York, 369 pp.; suppl. scient. edit.)

821 but there can be no doubt that flight itself in some situations must cause a pronounced negative selection, namely for species living in small areas surrounded by unhabitable land or by water. The ± stenotopic species of certain altitudinous regions — often quite restricted — of higher mountains form excellent instances. Whether they are wooded or not has little importance; also pronounced forest insects are caught by the ascending convection currents as can be observed abundantly on the surface of snow-fields in higher alpine steps.

p. 364. Stability, restriction and isolation of habitats favour brachypterous species and forms; variability, extension and moderate splitting up of habitats favour macropterous species and forms. Thus in periods characterized by alternating stability and variability — above all concerning climate — dimorphic species are favoured. This is applicable to the Quaternary Period with its alternating glacial and interglacial epochs.

p. 365. All constantly brachypterous species have no doubt passed through a dimorphic stage (eventually before the origin of the present species) during which they were exposed to factors working in favour of flightless individuals. A complete elimination of a recessive gene like "macropterous", however, is not possible by means of selection alone, it must be due to the action of chance within small populations. In fact, the "macropterous gene" may be present in many species generally regarded as constantly brachypterous, and accidently the copulation of two heterozygotes may cause the appearance of a single macropterous individual, often termed as "atavism".

p. 366. The distribution of dimorphic forms. On the basis of 25 maps (fig. 28—53) an attempt was made to describe the late Quaternary history of some dimorphic Carabids in Fennoscandia. The foremost rule, clearly illustrated by *Calathus mollis* (fig. 28), is that macropterous individuals — "the parachutists" — are predominant at the periphery of the species; a preponderance of brachypterous individuals indicates an early colonized area. By this method it is possible to suggest for instance that *Calathus mollis* and *Harpalus picipennis* have invaded Öland (and Gotland) directly from the south and that *Olisthopus* must have reached Åland from Sweden.

p. 377. *Calathus erratus* (fig. 35) is of special interest because it shows that selection in the coast-land of western Norway does not work as a principle in favour of the brachypterous form.

p. 381. If two or more originally separate postglacial stocks of a dimorphic species have come in contact and fused together one may be able to detect the "joint" as a zone of more frequent macropterous individuals, e. g. in *Carabus clathratus* (fig. 38) and *Pterostichus lepidus* (fig. 37).

p. 383. In cases where the brachypterous form has caught up the macropterous one on all points of the periphery it is justifiable to state that the species in question has actually reached its existence limit, e. g. in *Pterostichus vulgaris* (fig. 39), *Bembidion lampros* (fig. 40), *B. gilvipes* (fig. 41).

p. 387. At first sight some species are perplexing which in the north of Finland posses a ± separate stem with high percentage of brachypterism, e. g. *Bembidion guttula* (fig. 42), *Pterostichus minor* (fig. 43), *P. strenuus* (fig. 47) and, above all, *Bembidion transparens* (fig. 45). One must assume a separate immi-

822 gration route from the surroundings of the White Sea (in *B. transparens* also from the north).

p. 395. The strongest preponderance of brachypterous forms in Fennoscandia is demonstrated by the western coastland of Norway. In three species, viz. *Pterostichus strenuus* (fig. 47), *Bembidion aeneum* (fig. 49) and *Notiophilus aquaticus* (fig. 53), the gene "macropterous" has apparently been totally lost, in others, e. g. *Bradycellus collaris* (fig. 48), *Notiophilus biguttatus* (fig. 52), macropterous individuals are extremely rare. Reasons are brought forward to show that this phenomenon can by no means be due to selective action in postglacial time. The only acceptable explanation is that the species in question were isolated during the Last Glaciation (Würm) within icefree refuges along the Norwegian coasts.

p. 401. An illustrating example is *Bembidion Grapei* (fig. 50). Its distribution in itself could give reasons for accepting the species as a postglacial immigrant into Fennoscandia from the east but the occurrence of brachypterous individuals gives a quite opposite picture. It is doubtless a glacial survivor in western Norway.

p. 411. During the glacial period the small, isolated coastal refuges formed islands of organic life where selection was strongly active in favour of flightless insects. During the initial and final phase of every glacial period, on the other hand, the enormous and in part also rapid changes of habitats were in favour of flying insects. So, in repeatedly glaciated areas wing-dimorphism must imply a considerable advantage to an insect.

p. 415. Among the dimorphic species treated, at least 9 may be regarded as "winterers" within the limits of Fennoscandia during the "Würm" period. The present distribution of these 9 species within the plant-regions of the fjelds (tab. 29) shows that only *Notiophilus aquaticus* is capable of living in high-arctic conditions. Five species have never been recorded above the forest limit. These facts strongly contradict prevalent ideas about the climatic conditions in Fennoscandia during the Last Glaciation.

Synthetic part.

p. 417. The definition of "area".† The idea of an animal or plant species occupying an area is a fiction. The areal limits are constructed lines joining the extreme (northernmost, highest etc.) finding places (or rather populations, if they can be established) of a species. In pronouncedly stenotopic species the area is especially disjunct. A hypothetical example by which one may imagine the real distribution of a stenotopic insect near its northern limit is given (fig. 54). The zoogeographical "areal limit" — marked with crosses — may be defined as the line up to which on suitable places the species in question occurs permanently.

p. 419. The reliability of distribution maps. It is impossible to get a complete picture of the range of a species. But the map must be "credible". A characteristic of this state is whether, during a considerable period of investigation, all new added localities organically fit into the former picture without "spoiling" it. According to this criterion the Carabid maps of this book are "credible" and thus suited to form a basis for zoogeographical discussions. An idea of the relative exploration of Coleoptera within Fennoscandia is given in fig. 55.

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†(in German = "Areal"; "area" is standing for this meaning throughout the translation (English summary excluded) and the terms "region" and "range" are avoided; cf. pp. 417, 813; suppl. scient. edit.).

823 A considerable defect of my distribution maps is that they do not figure the present state; they form the concentrated result of more than 100 years' collecting. The number of coleopterists, however, is not large enough to make tolerably complete maps within much shorter time possible. But the indisputable fact that nearly all recent faunistical changes within the Fennoscandian area have been of a positive nature, i. e. have implied an extension of area, reduces the errors considerably.

For many species it would be valuable to make quantitative maps. Fig. 56 is an attempt to realize this on *Miscodera arctica* and makes the northern character of this species clearer.

It is maintained that the "point-method" of constructing distribution maps is, owing to its exactness, superior to every other and that not more than one species should be figured on each map. Otherwise the main advantages of mapping in comparison with a descriptive text are lost.

Some exemples are given in order to show that, in spite of the quantitatively extremely fragmentary experience of the actual fauna obtained by the collecting entomologist, he catches notwithstanding this fact a surprisingly high percentage of the actually occurring species.

p. 430. The relationships of the Fennoscandian fauna. Only two Carabid species *(Bembidion scandicum, Bradycellus ponderosus)* are unknown outside Fennoscandia. Otherwise it is clear that maps of the total distribution of each species would be of great importance for determining its history. Owing to the impossibility of checking the frequently conflicting foreign data, I simply have not ventured, however, to construct maps of the total area of any Carabid species.

The collective mapping of the total of Fennoscandian Carabids (362 species) occurring in other parts of Europe (fig. 58) or of the world (fig. 59) is less dangerous. The wide distribution of many species eastward into Siberia is striking, especially against the background of the distribution of species numbers within the limits of Fennoscandia (fig. 60). As would be expected, the powers of dispersal† (of flight) are as a rule better developed the wider the distribution of a species is (diagr. 47).

p. 436. Species distribution among different plant regions. The regions of Fennoscandia established by botanists mainly on the basis of forest vegetation — here partly termed with simplified names — are seen on the map fig. 61, the distribution of Carabid species within these regions in table 30. The summary (p. 448) above all gives an impression of the poor fauna of the Fennoscandian *regio alpina*.

Existence factors.

p. 449. Climate. It is generally — and rightly — assumed that climatic factors have the greatest importance in limiting the areas of animal and plant species. Biological and climatological investigations of recent years have shown, however, that the common meteorological figures — as representatives of the "macroclimate" — have only a restricted applicability to the factors actually operating, especially for the terrestrial ground fauna. The "microclimate" (the climate of and within square metres) is here decisive. Frequently it is suitable to work with an intermediate conception, the "lococlimate", which could be defined as the climate of hundreds of square metres.

p. 450. Temperature. The common method is to seek for connections be-

†(= "capability of dispersal" throughout the translation; cf. p. 15 of Part I; suppl. scient. edit.).

824 tween biogeographical limits and some isotherm of an average monthly temperature. For other than summer months this is rather unsatisfying; of all the months only the warmest one, in Europe July, is — from a biological point of view — tolerably characterized by its mean temperature.

An isotherm map of July is given in fig. 63. It shows the following ± pronounced plus-districts: 1. SE-Norway; 2. Gudbrands and adjacent valleys in eastern C-Norway; 3. the innermost part of Sognefjord; 4. the lake district (especially at Mälaren and Hjälmaren) of C-Sweden; 5. the inner parts of S Finland; 6. the surroundings of the northern end of the Gulf of Bothnia. All these districts are, to a ± high degree, indicated by the occurrence of southern — apparently heat-requiring — species. Above all the Central Swedish lake district has a markedly rich fauna including species with a ± isolated occurrence in this region situated north of the main area. In the cases of *Demetrias imperialis* and *Oodes gracilis* the interpretation as relics from a warmer postglacial period is inevitable. Some of these species were shown experimentally to have a high temperature preferendum (diagr. 48).

In Finland the favourable thermal conditions in July, mainly in the inner parts and even in comparison with Sweden, find expression in the long series of species (p. 459) which in Finland reach considerably higher latitudes than west of the Gulf of Bothnia. To a lesser degree only this fact is dependent on better opportunities for immigration in Finland.

p. 462. Minus-districts, as regards the July temperature, are: 1. the western and northern coast of Norway; 2. the upland of S-Sweden; 3. the fjeld region. The two first-named districts show so many other climatic pecularities (vide e. g. p. 467) that it is difficult to decide to what extent species are really excluded by the low summer temperature. Concerning the true fjeld-coleoptera especially the preferenda experiments made by Krogerus have shown that they are clearly heat-avoiding and thus may be restricted to alpine and subalpine habitats by the influence of the summer warmth.

p. 467. The temperature in spring and autumn. During these "critical periods" of insect life the minimum temperature must be of special importance. It is an expression for factors controlling the annual period of activity of poikilothermic animals. To a large extent the minima (fig. 64—69) follow the media (fig. 70, 71) but the favoured situation e. g. of the Norwegian coast land is more pronounced. It is therefore exceedingly probable that the numerous species ascending along the Scandinavian westcoast to high latitudes, but wanting in the inland, are dependent mainly on the spring and autumn temperatures. This assumption is strongly confirmed by the observation (already made by S. G. Larsson 1939) that Scandinavian Carabids with a pronouncedly western distribution include a strikingly high percentage of species hibernating as larva. It can be shown that some of these species in the easternmost parts of Fennoscandia — in East-Carelia — have in part changed to imaginal hibernation.

p. 479. Duration and frequency figures of temperature. In Fennoscandia especially Enquist has worked with "heat-sums" and constructed "thermo-isochrones" joining places with the same frequencies of days exceeding or falling below a chosen minimum or maximum. He compares these lines with plant-limits for which he pretends thus to find the controlling factor, e. g. in the case of *Picea abies* (1933, p. 207): "For the spruce growing spontaneously the

825 maximum temperature must amount to at least + 12.5° C during 65 days altogether" (translated from German).

Many botanists have enthusiastically accepted the ideas of ENQUIST, but he has also encountered severe opposition (vide LANGLET 1935). The most important objections against his method seem to be: 1. Even ENQUIST's figures are mean values and thus no real "factors"; they were calculated from a series of years with considerably varying figures (diagr. 49, table 32). 2. ENQUIST thinks it possible to find the deciding "factor" by establishing the point of intersection of the frequency curves from two stations situated at the plant-limit in question. Every investigator without preconceived opinions had found a common intersection point of *more than two curves* necessary. 3. It is absurd that the frequency values *alone* should determine the distribution of a plant species; the amount of heat during the annual period of activity cannot be insignificant. 4. The thermoisochrones of ENQUIST are drawn with more detail than is allowable from the thinly scattered meteorological stations. 5. The series of years used for different stations are not synchronous. 6. All meteorological figures used by ENQUIST are clearly *macroclimatic* and thus at most to a quite restricted extent applicable for biological purposes.

p. 485. *Precipitation and humidity.* The amount of precipitation in Fennoscandia shows a markedly unequal distribution (fig. 73). Its direct biological influence is mainly negative and unimportant but it works to a greater extent indirectly, causing humidity and ground moisture. It is quite probable that these factors are, at least partly, responsible for the absence of several ± clearly xerophilous species in Norway west of the Scandinavian main watershed. The experiments especially with the "limestone-species" (p. 128 a. f.) have clearly demonstrated how pronouncedly most Carabids react to moisture and humidity, so there can be no doubt as to their biological importance. In the Fennoscandian climate, however, they play an ecological rather than a geographical rôle, i. e. they regulate more the micro- and loco- than the macro-distribution. Above all the capability of otherwise pronouncedly forest species to live in an oceanic climate even on open grounds is remarkable.

As the thermic and hygric factors constantly work together many authors have tried to discover some *index* expressing in one figure for instance the difference between an oceanic and a continental climate. Fig. 74 shows the distribution of "Humidität"-figures (acc. to MARTONNE) and fig. 75 that of "oceanity-indices" (acc. to KOTILAINEN) in Fennoscandia. The low figures of SE Norway in fig. 75 are striking.

The persistence of the *snow-covering* also depends on the combined action of temperature and precipitation. As a thermo-isolator the snow plays an important rôle for the hibernating stage but its amount and duration is strongly locally determined. An attempt to illustrate in the form of an isochrone-map the distribution of frosty days without snow gave no regular picture.

p. 494. The *wind* is of great importance to the Carabids as a means of dispersal (p. 583) but seems to have little influence as an area-limiting factor. In regularly flying forms like the Lepidoptera it is different.

p. 495. The numerous heliophilous species among the Carabidae are highly dependent for their normal activities on *insolation* — the number of sunny hours — especially in the summer half-year. Fig. 76 shows pronounced plus-figures i. a. in

826 the Baltic coastal districts and the negative influence of the oceanic climate in the west. *Agonum sexpunctatum* forms the best instance of a species presumably excluded from these parts owing to the lack of sunshine.

p. 498. Future investigations on the influence of climate on the organisms will have to work in the field of loco- and microclimate and thus belong to ecology rather than to biogeography. No-one will succeed in mapping exactly a climatic factor deciding the distribution of a plant or an animal. From the common macroclimatic maps it is allowable merely to suggest in what domain (e. g. summer temperature, humidity, insolation) this factor has to be searched for.

p. 501. It may be possible to study the biological influence of climate also in an indirect way — e. g. by means of phenological observations on the annual aspects of vegetation. One would expect to find in this way a relative expression of the annual period of biological activity in a place or province. I have tried to construct such maps on the basis of plant-phenological material available for Sweden but the figures obtained proved too irregular to make the result surveyable without unallowable generalisations.

p. 503. Ground. The Carabids, as — with few exceptions — true "geophiles", are highly dependent on ground conditions, i. e. on edaphic factors, the hygric, thermic, mechanical and chemical qualities. The hygric and thermic factors were treated above (pp. 177 a. f.; 485).

p. 504. The mechanical properties of loose soil are mainly determined by the particle dimensions. Some few experiments (diagr. 51, 52) showed that particularly Carabids with digging habits are in many cases sensitive to this factor, avoiding too coarse sand. In the field it is especially easy to observe how the riparian fauna changes according to the particle dimensions of the shore material. This may, however, partly be caused by indirect — hygric and thermic — influences. Clay[†] (fig. 78), and to a restricted degree also different sorts of sand (fig. 77), has so characteristic a distribution in Fennoscandia that a correspondingly restricted area of stenotopic species would be expected. In fact, this has proved to be the case, especially for clay-bound Carabids. But clay also affects the organisms indirectly creating the conditions for eutrophic waters (p. 527).

p. 516. The chemical properties of the soil were partly dealt with under the heading of "limestone-species" (p. 112 a. f.) which proved to be chemically independent of $CaCO_3$. On the other hand it has long been well-known that certain insects, among them several Carabids, react positively to NaCl. A distinction was made between halobiontic (salt-demanding) and halophilous (salt-preferring) animals. Only 5 true halobionts occur in Fennoscandia, viz. *Anisodactylus poeciloides, Dichirotrichus pubescens, Dyschirius chalceus, D. salinus, Pogonus luridipennis;* possibly *Aëpus marinus* and *Trechus fulvus* also belong here. The undeterminated number of "halophils" includes species confined to sandy shores (independent of NaCl) and 3 species of *Bembidion (aeneum, minimum, fumigatum)* the two first-named of which through experiments proved to react positively to NaCl. *B. aeneum* has an inland distribution in Scandinavia conforming very well to the occurrence of Yoldia-clay (fig. 80) supposed still to contain small quantities of NaCl. The 3 *Bembidion* mentioned are probably real halobionts but demanding a quite small percentage of salt only. It should be considered whether the term "halophilous" merits to be maintained at all. Then it ought to mean that a certain species "loves" NaCl — not the seashore — and it is difficult

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[†](= "loam", in the sense of Lindroth; suppl. scient. edit.).

827 to understand how it could "love" NaCl without demanding it, maybe in very small quantities.

p. 525. It is not so easy to demonstrate an actual demand for other chemicals among Carabidae. It was supposed, however, that some ± synanthropous species would be favoured by artificial manure and that this would explain the rapid dispersal in later years shown by certain among them. As a suitable representative I chose *Amara ingenua* for experimental treatment and used as "standard" the culture-indifferent (or rather -avoiding) *A. praetermissa.* None of the species showed any positive reaction to the commonly used sorts of artificial manure (regarding *A. ingenua* cf. p. 539).

p. 527. A considerable biological importance is nowadays — especially by the botanists — attached to the soil-acidity constantly expressed as pH-figures. In the case of "limestone-Carabids", however, which could be expected to be "alkalophilous", the experiments showed the complete indifference of the insects. On the other hand Krogerus has demonstrated that several hygrophilous insects — also Carabids — are clearly "stenoionous", i. e. restricted to habitats with either high or low pH-value. But most hygrophilous Carabids are likewise indifferent. The alkalophilous species are bound to eutrophic waters and it is possible that they are in reality dependent on some other factor so that the pH should be estimated merely as an indicator. In acidophilous species (e. g. *Agonum ericeti* a. o. peat-bog insects) the connection with pH may be firmer.

p. 528. 3 Carabid species seem to be chemically dependent on (in any case positively influenced by) burnt wood.

p. 529. The term petrophilous was created by Holdhaus to indicate animals living on firm rock-ground only, or on soil lying in undisturbed position and directly originating from the rock. He thinks this fixed connection to the habitat is mainly due to its special content of nutriment, i. e. having in the first place a chemical explanation. In my experience on Fennoscandian Carabids the thermic and hygric qualities of the soil have a far greater influence than the chemical ones and only experiments would convince me that other rules are determining in the Alps.

p. 531. Nutriment. Carabids are generally regarded as pronouncedly carnivorous insects, divergent observations — mainly on species of *Amara, Harpalus,* av above all on *Zabrus* — being understood as exceptions. A complete collection of all the data available gives, however. a different picture. Out of 362 Fennoscandian Carabids:

99 species (incl. 31 under confinement only) proved able to feed on animal stuffs;

85 species (incl. 40 under confinement only) proved able to feed on vegetables. Of these species (138 in number) 48 were shown to feed on both sorts. It is permissible to suppose that Carabids are as a rule omnivorous. The zoophagous species, furthermore, generally do not attack living prey but merely wounded or newly dead animals. The rôle commonly attributed to Carabids as predators of great importance for controlling injurious insects and on the whole in the "natural equilibrium", seems thus overestimated. On the other hand the larvae, the normal nutriment of which is quite imperfectly known, seem to be more pronounced zoophages.

p. 538. The food habits of a species have a zoogeographical significance only if it

828 can be shown that it lives ± monophagous on, or at least clearly prefers, one single animal or plant. I. a. it might be supposed that many ± synanthropous species would be dependent on Crucifers and other weeds growing on cultivated soil. As an experimental object I chose *Amara ingenua,* exposing it to fruits and seeds of several common weeds (table 33). It proved clearly to prefer the fruits of Polygonum aviculare but was otherwise pronouncedly polyphagous.

Other Carabids are ± connected with special plants, e. g. *Zabrus tenebrioides* with cereals, *Bembidion nigricorne* and *Bradycellus similis* with Calluna, *Amara aulica* with Composites, several *Dromius* species with different tree species, *Calosoma inquisitor* with Quercus, etc. But in no case may the plant in question be regarded as the deciding factor restricting the area of the Carabid species.

p. 545. In a few cases there seems to exist a fix connection between a Carabid and its animal prey. The aggregation of most *Dyschirius* species with different *Bledius* is wellknown. Experiments on the behaviour of *D. obscurus* and *D. thoracicus* towards *B. arenarius* showed that they exhibit no greater attraction to *Bledius* than to other insects but react as polyphagous carnivores. A primary factor for the thriving of *Dyschirius* is no doubt the soil-condition (above all particle dimension and moisture) and their dependence on *Bledius* is due to the fact that on the suitable, sterile habitats these insects often constitute the single constant inhabitants fit for prey.

p. 548. *Brachynus crepitans.* It is supposed that the larva lives parasitically on some unknown insect host, as is the case with the American *B. janthinipennis.* At present the only thing that can be said is that this host is *not* *Agonum dorsale.*

p. 550. Also in the 3 Fennoscandian species of the genus *Lebia* — within which parasitic larvae occur abroad — the development is quite imperfectly known. It is probable that at least *L. crux-minor* and *L. chlorocephala* are dependent on Chrysomelids but are able to live as larvae on more than one host species.

Mollusc-eating species and those ± firmly bound to the nests of mammals seem in no case to be dependent on a single animal species.

So the food-factor as a whole is of very little importance as restricting the distribution of Carabids.

p. 554. *Competition.* This is the ecological factor most difficult to understand concretely. As a proof of the increased competition between closely related animals Elton has stated that the average number of species per genus in restricted habitats is smaller than in more extended faunal districts. Williams opposes this conception by demonstrating that an arrangement of genera with 1, 2 etc. species forms a logarithmic series. The Fennoscandian Carabid fauna agrees rather well with this (diagr. 53). From this it follows that in small samples automatically a smaller average number of species per genus must be expected. A treatment of samples from some restricted riparian habitats in Sweden (table 35)) shows that the average figure mentioned is constantly ± *higher* than expected and thus clearly contradicts Elton's conception that competition is increased between taxonomically related species. It is, besides, a common experience of field-entomologists that Carabid genera (e. g. *Harpalus, Amara, Dromius*) are often abundantly rich in species on quite restricted areas. The competition for food and space ought to play an exceedingly modest role among Carabids. The only case hitherto known, of supposed competition — or better, of one-sided "enmity" — between two Carabids is that of *Carabus nemoralis* contra *C. hortensis.*

829 p. 560. Enemies. The number of animals affecting Carabids as predators and parasites is high, but they are little specialized; no enemy seems to be restricted to a single Carabid species. The area-restricting effect of enemies if very unimportant.

p. 563. Stenotopie and eurytopie. The zoogeographical significance of a stenotopic habit is naturally dependant on the ± common occurrence of the habitat in question. E. g. a forest-species may be continuously distributed in N-Europe but have a highly disjunct area farther south. A sparse occurrence of suitable habitats also affects the chance of dispersal. A special interest is connected with species which are ± clearly eurytopic in the centre of their area but towards the periphery gradually become stenotopic (e. g. northern species on fens in C. Europe), a very intelligible effect of the "minimum rule", mainly dependent on microclimate.

p. 568. Types of development. Most Carabids hibernate as imago, the exceptions — the ± regular larval hibernators — constituting merely about 20 percent of the Fennoscandian fauna. It is proposed to designate these types, not as S. G. Larsson (1939) according to the time of propagation with "F" (spring-insect) and "H" (autumn-insect) respectively, but according to the hibernation stage as I- and L-type (imago- and larval hibernator respectively); quite irregular species were termed as 0-(zero-)type. The zoogeographical significance of the hibernation type mainly concerns the influence of climate and was treated above (p. 475).

Dynamic factors.

p. 573. Flight power and wind dispersal. The Fennoscandian Carabid fauna consists of 3 dynamic elements: constantly flightless 49 species (13.5 percent); constantly able to fly 263 species (72.7 percent), among these 177 species observed flying; functionally dimorphic 50 species (13.8 percent; vide p. 335 a. f.).

Flight is a normal, daily function only for 9 species, belonging to *Cicindela* or the subg. *Bracteon* and *Chrysobracteon* of gen. *Bembidion.* The remaining flying forms use their wings only at certain seasons, the imago-hibernators mainly in spring, the larval hibernators — which fly on the whole more seldom — in the summer (diagr. 54). The flight of Carabidae seems to have no sexual function but its main task is to facilitate the change of quarter, especially for the imago-hibernators in spring. Riparian species living by fresh water (of which only *Elaphrus angusticollis* is constantly flightless) may be on the wing more frequently owing to inundation or drying up of their normal habitat also in summer.

p. 583. The Carabids — with the exception of the 9 species named above (p. 579) — are weak flyers, their flight-direction being highly influenced by wind. So they are good objects for an anemochorous transport. For a dispersal over long distances to be realized this transport must take place at high altitudes. In later years the "aerial plankton" has been the object of careful studies by means of aeroplanes, especially in U.S.A. (Glick 1939). The figures obtained by these investigations are illustrated by means of 3 diagrams (55—57). Carabids were also present, up to 3000 metres, all flying forms. Nevertheless a dispersal of Carabids through the upper air ought to play a very modest rôle: they are non-parthenogenetic insects seldom swarming gregariously; they have proved — in connection with anemo-hydrochorous transport — to follow the winds prevailing near the

830 earth surface; their actual distribution shows no disjunctions referable to the dispersal "by leaps" expected on the assumption of high-air dispersal. The insignificance of all sorts of wind-dispersal of flightless Carabids (incl. earlier stages) is clearly demonstrated by the distribution of dimorphic species (p. 366 a. f.). An interesting fact is that the 9 best flyers among Carabids *(Cicindela, Bembidion;* above, p. 579) show strong geographical conservatism, obviously because they are able to direct their flight actively.

p. 592. As previously described (p. 256) the flight-direction of Carabids (and other insects) may also be influenced by sun. Species flying in the evening seem inclined to direct themselves toward the west and accordingly 4 cases are known of Carabids which have crossed the Bothnian Bay from Finland to Sweden, but none in the opposite direction.

p. 595. The question of whether fertilized females do regularly fly is very important, because this would mean an immensely increased chance of colonizing new areas. No females obtained flying in the field proved to be fertilized. But in two cases I succeeded in forcing by means of artificial light a female of *Oodes gracilis* to fly after copulation, after which she deposited fertile eggs. After all this seems, however, to be a rare exception as is demonstrated i. a. by the distribution of dimorphic Carabids.

p. 598. Water-dispersal. Carabids are comparatively well suited for water-transport as they float high on the surface and thus are able to keep respiration-air under their elytra for a long time. Their power of resistance is greater at low temperatures (i. e. in the winter half-year) and especially in fresh and slightly salt water (compared with the ocean water). The Baltic thus makes a fairly surmountable obstacle for hydrochorous insects. The most effective form of water-transport is with drift-ice in the spring, especially with rivers. This would be worth a closer investigation by means of planting out some foreign riparian species on a short bank-stretch on one of the larger Scandinavian rivers.

p. 604. The most effective dispersal method is anemo-hydrochorous transport, excellently described by PALMÉN (1944). Its main advantage is the concentration of wind-spread animals within small areas, the shores, and the correspondingly increased chance of propagation within the new territory.

p. 605. Transport by animals. Only birds have to be seriously regarded in this connection. Carabids, however, are extremely badly adapted to attach themselves to birds, so this method of dispersal seems at the very most to deserve consideration only in the case of *Demetrias monostigma,* a species with pronouncedly disjunct area and possessing effective clinging-organs in its suckerbearing tarsi.

p. 606. Transport by man. Merely two Carabids are "anthropobiont" and therefore must be regarded as introduced into Fennoscandia *(Pristonychus, Sphodrus).* For some other species, the most interesting of which is *Carabus nemoralis* (vide p. 632), the same explanation is at least a high probability. That the importance of introduction by man is often overestimated i. a. becomes evident from the fact that, in spite of the intense traffic, from N. America only 3, from the temperate parts of the southern hemisphere not one, introduced species have been definitely established as members of the non-synanthropous European fauna.

p. 609. As a dynamic factor often a proposed "desire" of the animal to expand

831 its distributional area is maintained, an extremely misleading term. The active movements of the individual are mainly due to feelings of "discomfort" in its prevailing surroundings and it will certainly stop its migration as soon as it finds a place in all respects suitable. Such a thing as a collective "want" of the species to colonize the whole habitable area of course do not exist. Nevertheless the result mentioned may be approximately reached by a combination of adequate time, of chance and of sufficient powers of dispersal.

p. 610. The barriers against dispersal. In Fennoscandia the sea and the higher mountains form the most evident obstacles. Of course they are most effective for flightless forms. A comparison was made on the area-limiting effect of 3 sea-regions, viz. the Gulf of Finland ($>$ 45 kilometres), the sea between Denmark and S-Sweden ($>$ 4 kilometres), the Channel ($>$ 31 kilometres). In spite of the greater distance the first-named of these sea-regions, proved to form the least difficult obstacle to Carabids which is probably mainly due to the considerably lesser amount of salt in its water, facilitating an anemohydrochorous transport.

p. 613. The main Scandinavian watershed from southernmost Norway to N-Finland forms a remarkable barrier for many species. The passes situated below the *regio alpina* and shown on the map fig. 61 (p. 437) have played a considerable positive rôle, especially during the postglacial climatic optimum. It is interesting to note that also flying forms are to a great extent dependent on the passes for crossing the fjeld-range, a further proof of the small effect of dispersal through the air in high altitudes.

p. 616. Final remarks on area-limits. In practice it is often very difficult to separate existence limits and dynamic limits. The latter may be distinguished by the following characteristics: the species is still in demonstrable expansion (e. g. *Amara majuscula*, p. 622); the peripheral area is characterized by decreasing abundance but not necessarily by decreasing frequency (existence limits may be expected to demonstrate a contrary picture); after excluding all possibilities of existence-factors forming the limit, this may — provisionally — be regarded as determined by dynamic factors.

The clearest existence limits of Fennoscandia are the northern limits of southern species. Fig. 82 gives a general idea of their course in the central parts of the region.

The history of the fauna.

p. 621. The changes of fauna in recent times. The additions to the Fennoscandian Carabid fauna during the last hundred years are numerous and, naturally, mainly due to intensified investigations. There is, however, quite a series of species which must in fact have invaded the area during the short period of some few decades. Those species may be termed transgrading which occur ± regularly but presumably are not permanent inhabitants of Fennoscandia; a good example is *Calosoma sycophanta*. The clearest case of a late immigrant, now native, is *Amara majuscula* (fig. 83, 84), in Sweden also *Harpalus puncticeps* (fig. 85). *H. rupicola* is doubtful, occurring in Gotland and Öland only.

p. 628. Old species with ± distinct areal expansion in "historical" time are figured on the maps fig. 86—90. Of special interest also is *Carabus nemoralis*, supposed to be originally introduced by man. *Harpalus punctatulus* is remarkable

832 in having extended considerably in Finland, but stationary — though possibly with increased abundance — in Sweden.

p. 635. Some few species seem to have decreased in recent time, e. g. *Agonum Bogemanni* and *Harpalus nigritarsis*. In part they may be culture-avoiding.

p. 636. The causes of late faunal changes. It is shown that the — in part very rapid — expansion of species-areas in recent times cannot be an exponent of the normal postglacial immigration to Fennoscandia. There must be special reasons for the remarkable behaviour of these insects. In many cases man is responsible for the changes in fauna, not so much because of direct introduction of new species (vide above, p. 606) as through the revolutionary transformation of the landscape — of the habitats — caused by him. Especially the formerly uniform forest districts of the North have been enriched by man with new habitats, and consequently with new insect species. The negative influence, through cultivation of the soil, is more marked in the South. Some habitats, with their fauna, are severely threatened in the whole of Fennoscandia, especially the river banks owing to water-power installations. In comparison with these changes of habitats the reduction of species by the activity of collectors plays quite an unimportant rôle.

p. 641. Changes in fauna may also be due to recent changes of climate. Such have been established beyond all doubt, causing — in the main — an amelioration of the North-European climate during the last decades. The Finnish zoologists (e. g. O. KALELA) especially have drawn conclusions as to the contemporaneous expansion of area of several animals. It has been stated that the increase of temperature has been greater in winter and spring than during summer and autumn. So far one has worked with average monthly temperatures only, but it is evident that, especially in spring, the minima must be of greater biological importance. The diagrams (diagr. 58—61) show that April is characterized by the greatest rise of temperature, that this rise is more marked in the minima than in the mean temperature, and finally, that not all parts of Scandinavia have been equally favoured. The last-named fact is more clearly demonstrated by the maps fig. 91 and 92. It seems possible to refer the expansion of area of some species, especially in central and northern Sweden, to the climatic changes mentioned.

p. 653. An immigration of insects into Fennoscandia may be caused by environment changes taking place in foreign parts of the species area. Drainage of lakes and fens — caused by man or by climate — has been thought to lead to the immigration into Fennoscandia of some water-birds from the East and it is possible that the same may be applicable to certain hygrophilous Carabids. That an increase of population density could give a similar effect seems improbable in the case of Carabidae.

p. 654. An expansion of area may be dependent on changed ecology of the species, eventually due to a new mutant. Several Carabids have adapted themselves to ± synanthropous conditions but it is at present impossible to decide whether this premises an altered hereditary constitution. No strict "ecotypes" (biotypes) could hitherto be detected in any Fennoscandian Carabid species.

p. 656. The foregoing chapter has no doubt given an impression of the unexpectedly great changes which have affected the fauna during the short period of a century. One might thus despair as to whether an attempt to reveal the whole

833 postglacial period would not be but a series of hypothetical guesses. On the other hand it must be remembered that surely no century during the whole geological evolution has, thanks to man, brought so many biological changes as the last one.

p. 656. Fossil finds. The Quaternary insect fossils of Skåne and Denmark have been carefully treated by HENRIKSEN (1933) but from the rest of Fennoscandia there are few finds only. Some new find-localities are described. The fossils reported from Finland by POPPIUS (1911) have proved to be unsatisfactorily determined; unfortunately the material (MH) was only partly available. A scheme of the late- and postglacial evolution of Fennoscandia (table 36) and a map of the finding-places for fossils (fig. 93) are given.

p. 665. List of fossil Carabids found in Fennoscandia and Denmark. The species follow in alphabetical order. For finds made in other parts of Europe, vide part I of this work and the supplement in this part.

Altogether 67 Carabid species (19 percent of the recent Fennoscandian fauna) are found fossil in Fennoscandia or Denmark; in addition 7 species (among these 3 supposed to be totally extinct) now absent from the area. Some conclusions are allowable: In preglacial time there lived in Fennoscandia — if period and insect are correctly determined — in part other species than now. In the last interglacial, on the contrary, the fauna had a quite recent stamp and demonstrates moreover that the climate was in part at least as warm as now (LINDROTH 1948 a). During the last glaciation (Würm) an alpine fauna, containing many characteristic members of the Fennoscandian regio alpina, but also some few species of a southern (alpine-subalpine) or eastern type now absent from the area, lived at the southern margin of the maximum ice-sheet. In postglacial time the climatic optimum allowed some Carabids to extend, at least slightly, beyond their present northern limit *(Calosoma sycophanta, Oodes helopioides, Pterostichus niger)*. An instructive example of how the fossil finds join the partly scattered recent localities of a species is given by *Agonum Thoreyi* (fig. 95).

p. 676. An extremely important question for judging the value of and the conclusion made from fossil finds is, to what extent one may calculate upon the constancy of the ecological valence† of a species, i. e. upon the firmness of its ecological demands. In fact it is impossible to deny that a change may occur, and it therefore seems incorrect to make conclusions about ancient climate etc. on the basis of one single fossil species. On the other hand it is quite justifiable to arrive at such results if quite a group of fossil organisms tends in the same direction.

p. 677. Relicts. This term by different authors has been used in a rather varying — wider or narrower — sense, the best one formulated by EKMAN (1915, 1922, 1935). Especially in limnic zoogeography, and also in phytogeography, a group called pseudorelicts (secundorelicts) was generally removed from "true relicts" on the plea that its members have not persisted *in situ* from the time of their isolation but undertaken ± extensive migrations from the original relict place. It is here maintained that such a distinction cannot be realized on the terrestrial fauna. The uninterrupted persistence of freely mobile animals in one and the same locality during thousands of years can in no case be proved. Consequently it seems necessary to use the word "relict" in a wider sense. The

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†(= "valency"; suppl. scient. edit.).

834 following definition is proposed: A population (or stock) of a genetic and taxonomic unit (subspecies, species, genus etc.) is a relict if it is functionally separated from the remaining (as a rule wider, possibly prehistoric) area of the unit and was not able to invade the isolate during present natural conditions.

In order to present material supposed to include typical relicts a list of the most isolated localities or locality-groups among Fennoscandian Carabid species was put together (table 37). In each case a remark on the supposed cause of isolation was added.

The different sorts of relicts may be designated according to the factor the change of which in earlier times caused the separation from the remaining area. A. Cold-relicts, e. g. *Nebria Gyllenhali* in central S-Sweden and Gotland, *Pterostichus adstrictus* in Småland; also the Cerambycid beetle *Evodinus interrogationis* L. (fig. 96). It is made probable that these relicts — or the main part of them — emanate from the early postglacial southern immigrants and not from a later period of climate-deterioration. — B. Heat-relicts. These are particularly numerous within the lake-district of central Sweden (e. g. *Demetrias imperialis, Oodes gracilis),* as well as in Öland and Gotland (several *Harpalus* species), but occur also in S-Norway (e. g. *Abax ater*), in the inner Sogn district (cf. p. 454), at the northernmost part of the Bothnian Bay etc. The great number of heat-relicts is easily understood as a result of the postglacial climatic optimum, the far-reaching effect of which in Fennoscandia was clearly demonstrated on fossil plants. — C. Coastal relicts. Owing to the considerable, mainly negative fluctuations of shore-line in Fennoscandia in postglacial time the premises for seashore species being left behind and persisting on fresh-water shores are given. The best examples of such relicts are *Cicindela maritima* and *Dyschirius obscurus* in Finland (Krogerus 1932) and probably *Bembidion assimile* and *Dromius linearis* by the large Swedish lakes. — D. "Anti-culture-relicts". Pronounced examples are many forest-beetles, but mainly non-carabids. — E. Interglacial relicts. These have surived the last glaciation on isolated refuges at the ice-margin. Their history is treated in the following chapter.

p. 698. The postglacial immigration. Reliable conclusions on the faunal history must rest on paleoclimatological and geological facts. Unfortunately the opinions of authors within these domains are often contradictory, e. g. it still remains uncertain whether the Baltic in postglacial time had direct communication with the White Sea, or whether Öland-Gotland at any postglacial period stood in firm land-connection with the Central European continent. In principle traits, the postglacial evolution of Fennoscandia, however, seems clear. It is a question of general importance to what extent the biogeographer must feel himself bound by theories established by geologists etc. At any rate it must be regarded as absurd when Tanner (1937) declares that the problem of floral and faunal hibernation on glacial refuges must be solved by geologist alone. In fact geology has obtained many productive impulses from biogeographers. But the latter have to be fully conscious that they must be able to refer to whole series of biological facts before they are justified in opposing generally accepted geological opinions.

835 p. 704. The southern immigrants. The coleopterous fauna at the southern margin of the inland-ice during the last glaciation (i. e. in N-Germany and Jutland) had a northern-alpine character and so had the first postglacial immigrants in Skåne. Only two species of Coleoptera otherwise unknown from Fennoscandia are reported as participants in this group, but 6 or 7 which occurred in the north of the Central European continent at the Würm maximum are absent from the Central Europe of to-day. Apparently the northern Würm-ice did not extend southward far enough (viz. the ice of the Alps not northward) to make a complete "Mischfauna" of northern and southern elements possible. The alpine and subalpine species therefore after the Würm-ice began to retreat returned mainly the same way as they had come. The extensive fauna-exchange giving rise to the boreo-alpine type of distribution thus seems to have taken place in the Riss-period (the next-to-last main glaciation).

p. 710. There has been much discussion about the question of to what extent the present alpine-subalpine flora and fauna of Fennoscandia has been recruited from the group of the earliest immigrants (i. e. from the south). At present one seems generally inclined to deny any importance to this route, referring i. a. to the almost complete lack of alpine-subalpine fossils in Sweden north of Götaland. I agree with the conclusion but not always with the arguments. For it is often maintained that, owing to amelioration of climate, the ice-margin north of Skåne periodically retreated so rapidly that it was immediately followed by forest vegetation; — with a yearly retreat of 100 metres or more there must, however, constantly remain a considerable forest-free zone next to the ice, simply owing to the slow growth of trees. A destructive influence, especially on perennial alpine plants, was rather exerted by the permanent change of habitats and — on annual plants and animals — the barrier formed by the Närke-sound, at the southern shore of which the forest may have occupied the whole land before the northern shore became free from ice.

p. 714. It is often difficult to decide how far toward the north the tribe which immigrated over southern Sweden has reached in Scandinavia because it may secondarily have been confused with other tribes of the same species which had "hibernated" at the west-coast or, above all, with invaders from the east, over Finland. As a rule we find that in the case of "double" immigration (over Sweden and Finland respectively) the Finnish tribe almost constantly has reached more northern latitudes and often spread over to Sweden round the Bothnian Bay with a ± pronounced gap to the southern Swedish area. In some wing-dimorphic species it is possible to localize the "cicatrice" on the Swedish side of the boundary though the two tribes have already fused (p. 381). In two species only *(Agonum versutum, Synuchus nivalis)* it seems probable that they have reached the northern end of the Bothnian Bay by means of immigration through Sweden. But the fauna of North-Sweden (approximatively N of 64°) obviously has received few contributions by this way alone. Especially in Norway north of Tröndelag (about 65° N) the southern postglacial immigrants are very few.

p. 718. The eastern immigrants. Under this heading are included all species (or tribes) which have reached Fennoscandia in postglacial time from centres E of the Baltic. Owing to the rapid disappearance of inland-ice in eastern Fennoscandia this process could begin already before Yoldia Time. It seems obvious that alpine-subalpine organisms — in accordance with the conditions in

836 Scandinavia — were not able to reach the present fjeld region of Finland by means of postglacial immigration from the south, partly, however, from the north-east.

p. 719. The "Baltic" path of immigration over the Gulf of Finland was of great importance, mainly because of exclusively favourable conditions for an anemo-hydrochorous transport (PALMÉN 1944). Even E Sweden was touched by this immigration group, e. g. probably in the case of *Agonum longiventre*.

p. 721. The "Carelian" route of immigration, over land E of the Gulf, no doubt has provided Finland with the main part of its fauna. Many species have immigrated by the Baltic as well as the Carelian route and in these cases a hiatus of area may exist in the middle of the Finnish south-coast. It is important to point out, however, that such a gap may be dependent on climatic factors or on inequal exploration.

p. 724. An important immigration route has existed from the White Sea district over Kuusamo-Salla and westward. It has been used especially by ripicolous plants and insects and it was therefore supposed by some authors that in early postglacial time an uninterrupted sea-connection would have existed between the White Sea and the present Bothnian Bay at the shore of which some of the species in question still exist, often in a rather isolated position. A real breaking through of the watershed in Kuusamo-Salla seems, however, never to have occurred, but the separating isthmus had a breadth of some few kilometres only, thus forming no severe obstacle to dispersal of shore-organisms.

p. 728. Some wing-dimorphic species show that the Kuusamo-Salla immigration group was not simply an early vanguard of the "Carelians" but a functionally separated unity. In part its members may emanate from Kanin via the south-coast of Kola but the core of the group can hardly be interpreted except as the descendants from a glacial refuge somewhere in the vicinity of the western part of the present White Sea. It may be termed the "White Sea group".

p. 730. The "Kanin-Kola group", on the other hand, contains species originating from districts E of the White Sea (i. e. of the maximum Würm-ice limit) and contains mainly tundra forms restricted in present Fennoscandia to the Kola peninsula. Whether a postglacial land-connection Kanin-Kola has really existed is still an open question.

p. 732. It is difficult to decide how far to the south members of the eastern (northeastern) immigration group have reached in Scandinavia (cf. above, p. 715). *Tachyta nana*, however, seems to show the best example of a species which has expanded even to southernmost Sweden (Skåne) by this route. A list of species with an unusually distinct "double" — southern and eastern — origin is given (p. 734).

The problem of "Würm-hibernation".

p. 735. Probably Fennoscandia, like other parts of Europe, has been the object of 4 — or at least 3 — different glaciations; it seems impossible, however, to understand clearly the biological consequences of more than the last one, the Würm. Also during the maximum of this glaciation southwestern Jutland was free from ice, so it was early supposed (BLYTT 1893; SERNANDER 1896) that non-glaciated areas might have existed also on the Scandinavian west-coast. The

837 theory was developed mainly by botanists (Th. Fries 1913; Tengwall 1913; and, above all, Nordhagen 1933, 1935, 1936); the first zoologist seriously dealing with the problem was Wahlgren (1919).

p. 738. How is it possible to state that an animal or plant species is a "Würm-winterer"? It is suitable to start from *Simplocaria metallica,* a coleopterous species exposing its history with quite diagrammatic clarity (fig. 106). Its present distribution shows a restricted postglacial tribe in S-Finland but the clearly bicentric Scandinavian area without any doubt emanates from refuges during the Würm on the west-coast. An important feature is furthermore the total absence of a connection eastward into areas in N-Russia outside the boundary of the Würm-glaciation. The only Carabid constituting a similar case of distribution, and likewise an indisputable Würm-hibernator, is *Elaphrus lapponicus.*

p. 741. Lists are given of Carabid species the distribution of which agrees in one respect or other with that of the "model", *Simplocaria metallica.* Attention was paid to the following features: a) isolation of the Fennoscandian area especially toward the East; b) distinct hiatus between a southern postglacial tribe and the supposed hibernated one; c) bicentric Fennoscandian area.

p. 743. As previously shown (p. 397 a. f.) a few wing-dimorphic species are likewise indisputable glacial survivors in Fennoscandia. Some of them are representatives of characteristic types of distribution and it therefore seems justified to search for "hibernators" among non-dimorphic species agreeing in these respects. Thus 6 other Carabids belong to the type of *Bembidion aeneum,* 9 to that of *B. Grapei,* 7 to that of *Pterostichus strenuus* and *Bradycellus collaris.*

p. 745. Supposed glacial survivors may, however, belong to types of distribution not represented by dimorphic species. One is the West-Scandinavian type comprising on the one hand a few species perfectly restricted to western Norway (p. 791), on the other a more numerous group, the members of which reach much further toward the North along the Norwegian coast than in the inland. The lastnamed type is no doubt to a great extent shaped by climate but as soon as the species area expands into Sweden through the fjeld-passes in a non-oceanic climate (e. g. *Bembidion nitidulum, Leistus ferrugineus),* this cannot be the case. *Carabus coriaceus,* treated more in detail, has a South-Swedish tribe, due to postglacial immigration, but the Norwegian and Central Swedish area must emanate from some Norwegian glacial refuge; the latter area, at present very disjunct, probably was more continuous during Atlantic Time.

p. 748. Distinctly alpine-subalpine species — 16 in number — certainly all are Würm-hibernators. — *Bembidion Schüppeli* and *Dyschirius septentrionum,* demonstrating a striking resemblance in distribution, besides the "wintered" population have immigrated in common from the East by two different paths.

p. 749. The ± panfennoscandian type of distribution, represented among the wing-dimorphic species by *Notiophilus aquaticus,* have a multiple origin but in all cases ought to include also a hibernated element. Strictly speaking merely 3 species are panfennoscandian, in addition to the *Notiophilus* mentioned only *Calathus melanocephalus* and *Patrobus assimilis;* with somewhat restricted standards for ubiquitous distribution, however, a total of 31 Carabid species may be termed "panfennoscandian". It is a remarkable fact that no less than 13 of them (i. e. 42 percent) are functionally brachypterous, whereas within the whole

838 Fennoscandian fauna this group amounts only to 27 percent (max.). No other explanation seems possible than that species widely distributed ("panfennoscandian") are in part descendants of populations living on the Würm refuges where selection worked in favour of flightless species and forms.

p. 752. Is it possible, from biogeographical facts, to determine the exact position of Fennoscandian Würm refuges? An attempt to do so was made, on the basis of the recent distribution of *Papaver* and other alpine plants, by Nordhagen. But already earlier the bicentric type of distribution in Scandinavia was considered by botanists to have emanated from two separate main refuge areas in Norway. For high-alpine organisms, however, the gap between the two "centres", situated within the lowest part of the fjeld-range where it is cut through by many passes (vide fig. 61), may be brought about by climate, especially during the postglacial climate optimum when the forest ascended about 300 metres above its present limit. A species like *Nebria nivalis* may have been severely disfavoured at that time. A bicentric distribution in less cold-requiring forms (e. g. *Simplocaria metallica, Elaphrus lapponicus),* on the other hand, must be due to historic factors. It was shown, furthermore, that the southern and northern population of bicentric Carabidae at most in exceptional cases may be regarded as postglacial immigrants from the South and the Nordeast respectively. Thus the idea generally entertained by botanists that a pronouncedly bicentric distribution in Fennoscandia is the sign of Würm-hibernation within two separate main areas holds good also for Carabids.

p. 757. The biological theory of localizing in detail the glacial refuges, maintained in North America by Fernald, and in Fennoscandia above all by Nordhagen, is based on the assumption that certain plant species ("rigid" species, Hultén 1937) are extremely conservative and have practically lost their power of dispersal in postglacial time. This idea, in fact, is something of a mystery and it would be highly desirable that some one could give it a more concrete basis by investigating — with experiments, too! — some typical "rigid" species according to their dispersal of diaspores, their ecological specialization, their competition power, their eventually reduced reproduction owing to population decrease (possibly combined with the "Sewall Wright effect" within small isolated populations). It seems to me, however, that Wynne-Edwards (1939) has clearly overestimated the stenotopic character of these species as being able to explain their restricted areas. In Carabids it is obvious that the power of dispersal — especially of flight — is the main factor controlling the geographical "conservatism" of species. This was clearly demonstrated by the study of wing-dimorphic species which can therefore contribute towards a localization of Würm-refuges.

p. 759. In the High North one refuge was supposed — on entomological grounds — by the White Sea, another in the neighbourhood of Petsamo — S-Varanger, probably below present sea level (Tanner 1937). The refuges proposed by Nordhagen on the Varanger peninsula, on the island of Mageröy, and at the mouth of Porsangerfjord, do not appear clearly from the present entomological material. But the largest of all "major refuges" assumed, the outer coastal districts from the mouth of Alta-fjord south to about the Arctic Circle, including the Lofoten Isles, has played an important rôle also in the history of the fauna, no less than 32 Carabids enumerated (p. 761) as proposed "winterers" here.

839 p. 761. Against the facts hitherto presented by botanists *Bembidion aeneum* and some few other species suggest a refuge also in the immediate vicinity of the Trondheim-fjord, and this is supported also by geological facts.

p. 762. In South Norway NORDHAGEN counts upon three separate refuges, in M ö r e, at the mouth of S o g n e - f j o r d, and, finally in R y f y lke. Only the first-mentioned is founded also on geological facts. Owing to the possibility of several species having reached these parts of Norway by means af postglacial immigration from the South and Southeast it is usually difficult to distinguish the true hibernators. No doubt, however, they have been more numerous than in any other "major refuge".

p. 763. In connection with the Sogn-refuge it is observed that this was established by NORDHAGEN on the basis of a l p i n e plants the present concentration of which in these areas may in part be due to the high-alpine character of Jotunheimen and adjacent fjelds, not only in present but likewise in interglacial time. For pronouncedly high-alpine organisms an interglacial period may be at least as dangerous as a glaciation. In these districts their Würm-hibernation may have taken place in part on nunataks.

p. 765. The southernmost refuge assumed by botanists, in the vicinity of R y-f y l k e, no doubt is an entomological reality too. I. a. the isolated presence of *Bembidion tibiale* finds no other acceptable solution. *B. harpaloides,* on the other hand, is probably a postglacial immigrant from "Dogger Land". The hibernators of the South-West are to a great extent constantly brachypterous, or dimorphic species occurring here exclusively or quite prevailingly in their flightless form. An unusually distinct case is formed by *Chrysomela crassicornis* (fig. 109), constantly brachypterous.

p. 769. The idea of a refuge a t t h e m o u t h o f O s l o - f j o r d is quite hypothetical, founded up to now on no reliable geological facts. On the other hand, the distribution of species like *Bembidion litorale* and *Perileptus areolatus* would be easier to understand on the assumption mentioned.

p. 772. An attempt to illustrate the possible localization and extension of the Fennoscandian Würm-refuges is made in map fig. 111. In its construction attention was paid not only to geological and biogeographical facts but also to the generally assumed lower position of the sea-level during the maximum glaciation.

p. 774. T h e c l i m a t i c c o n d i t i o n s d u r i n g t h e l a s t g l a c i a l p e r i o d. Table 38 (p. 802) gives a summary of the proposed glacial and postglacial history of each Carabid species. The number of glacial survivors lies between 52 and 130. The distribution of these species within the Fennoscandian plant regions (acc. to table 30, p. 440) shows that a b o u t h a l f t h e n u m b e r d o n o t o c c u r i n t h e r e g i o a l p i n a o f t h e p r e s e n t d a y; even among the "sure" hibernators — 52 in number — 44 percent (23 species) according to our present knowledge a r e n o t a b l e t o e n d u r e a n a r c t i c c l i m a t e. How is it possible to make this fact agree with current conceptions of climatic conditions during the Würm-glaciation?

p. 776. It is generally assumed that the temperature — not least in the summer — was lowered during the Würm to a degree of 3—8° C on an average (the last-named, higher figure in Central Europe acc. to KÖPPEN & WEGENER 1940). Applied to Fennoscandia this would mean that, following the smallest fall proposed, the Norwegian coast north of 62° did not reach + 10° C in July; if the

840 pessimistic view of Köppen & Wegener is right, no part of Fennoscandia had attained this figure.

p. 777. Under these circumstances the question of the constancy of ecological valence (treated above, p. 676) arises of itself: Is it not possible that the wintered species have altered their ecology? In fact, there seems to exist no reason why such changes should happen contemperaneously in whole series of species; above all one cannot imagine why an insensibility to cold, hypothetically obtained by selection during a glacial period, should be lost in postglacial time. — It thus seems reasonable to consider whether a glaciation may not arise by factors other than lowering of summer temperature, or whether the loco-climate on favoured places may not have compensated for deterioration of macroclimate.

p. 778. Some authors are of the opinion that a glaciation is induced more by means of an increase of snow-fall than by decreasing temperature. Above all the immense regression of glaciers in all part of the globe during the last decades has taught us that such a process can take place without considerable increase of summer temperature, but mainly owing to a lengthening of the yearly melting period. *Mutatis mutandis* this may be applicable also to a period with transgression of glaciers.

p. 780. The great importance to vegetation and animal life of places situated near inland ice but favoured by loco-climate is shown by examples from many parts of the globe among which the margin area of Vatnajökull on Iceland is more fully described (Lindroth 1931). It becomes quite clear that the immediate neighbourhood of inland ice by itself does not necessarily work destructively on organisms. The causes may be: 1. If the landscape is hilly, slopes with favourable exposure to sun may occur. 2. Marginal mountains and the ice itself may form wind shelter. 3. At sufficient niveau differences the winds originating from the high pressure over the ice may receive the character of thermic-favourable descending winds ("Föhn"-winds). Possibly it is due the failure of such winds that an especially severe glacial climate prevailed at the southern ice-margin in Central Europe (cf. p. 776). — It will easily be seen that the West-Norwegian coastal region is very favourably situated regarding the points mentioned above. To these comes the Gulf Stream which, no doubt, touched upon this coast also during the Würm. It is therefore by no means contradictory to "exact" science to assume that the Fennoscandian Würm-refuges were inhabited also by other than purely arctic (alpine) organisms.

p. 784. Quite recently Lindquist (1948) has brought forward the opinion that even the spruce *(Picea abies)* in a special form, described by him as "var. *arctica*", was a glacial survivor on the Norwegian coast. This conclusion seems to me premature, above all because the incomplete knowledge of the spruce populations in North Finland makes it impossible to decide how isolated the Scandinavian "var. *arctica*" is toward the east. Two lichens, brought forward by Lindquist as supporting his theory, cannot be of conclusive importance in this connection especially because of the extraordinarily strong power of dispersal characterizing these plants. In summary, a glacial survival of the spruce in Scandinavia is, if not quite impossible, still hardly probable; at any rate it is hitherto unproved.

841 p. 787. The distribution of some insects — not Carabids — may contribute to the question of whether the glacial refuges were provided with some tree vegetation. Thus *Curculio crux* (fig. 113) and *Rabocerus foveolatus* (fig. 114) must be regarded as doubtless "winterers", at least in northern Norway, and indicate the survival of shrub-formed *Salix* and *Betula*-trees respectively. It would be an extremely interesting task to treat, from ecological and biogeographical points of view, the insects feeding on all sorts of trees in Northern Fennoscandia.

p. 791. On the southern Norwegian refuges the glacial climate may be supposed to have been more favourable than in the extreme North — where nevertheless at least the birch survived — and thus the hibernation also of an atlantic (oceanic) faunal and floral element may be seriously considered. Here belong *Aëpus marinus* and *Trechus fulvus* (both flightless insects), among other Coleoptera e. g. *Otiorrhynchus porcatus* and *Mesites Tardyi.*

p. 793. It is of great interest in this connection to study the opinions of biogeographers concerning the history of the British fauna and flora. In that country the atlantic element is still more represented and in addition there occurs a "lusitanic" group of plants and animals with relations to the Iberian Peninsula.

It is a strange fact that in Great Britain — in this respect the most suitable country of Europe (Iceland perhaps excluded) — so little interest has been devoted by entomologists to biogeography. The best biogeographical survey of British Coleoptera has been made by a foreigner (Sainte-Claire Deville 1930 a). Quite recently, however, some attempts have been made to treat the faunal history of these islands on the basis of Lepidoptera (Ford 1945; Beirne 1947 b).

The paper of Beirne is very thorough but the results obtained by him are founded on extremely hypothetical premises. It is difficult to understand how he could venture to date the arrival of almost every British species of Macrolepidoptera from its present distribution alone. It seems that he has underestimated the importance of three things: 1. the influence of the environmental factors of the present time, especially the climate, in determining the range limits of species; 2. the changes of area which most species have undregone in postglacial time, mainly due to climatic changes; 3. — above all, the power of dispersal of Lepidoptera. A study of the Lepidopterous fauna of the island of Gotska Sandön in the Baltic (Jansson 1925, p. 124 a. f.), situated at a distance of 38 kilometres from the nearest land (the island Fårön) and totally of young postglacial age (above, p. 279), makes it clearly evident that by no means "migratory" species alone are capable of invading new land over sea stretches as wide as the Channel (> 31 kilometres). In fact, Lepidoptera — with few exceptions — are not favourable insects for solving the problems of fauna history.

Turning back to Beirne's paper it is of special interest to note that, to his mind, some "lusitanic" forms restricted to Ireland form the oldest element of the British fauna and according to him have survived the maximum glaciation within the area. Botanists also are now as a rule inclined to regard the corresponding element of the British flora as "hibernated". These species — animals and plants — are no doubt less cold-hardy than the trivial atlantic element represented in Norway. It may be permissible to conclude, by analogy, that a hibernation, as proposed above, was possible also for the major part of atlantic

842 animals and plants in Scandinavia. Probably owing to the distribution of land and sea they had better opportunities during interglacial time than at present to invade Scandinavia from the south.

p. 796. Whether man hibernated on the Fennoscandian Würm-refuges is still an open question not to be solved unless indisputably datable archaeological finds are present. The Komsa-culture, suggested by NORDHAGEN (1933, p. 82 a. f.) as glacial, was later estimated as postglacial (BØE & NUMMEDAL 1936).

p. 796. It is impossible on the basis of the Carabidae to decide whether some animals have survived more than one glacial period in Fennoscandia. The "west-arctic" element, represented by Lepidoptera and plants, seems to suggest this eventuality, at least for organisms enduring an arctic climate.

p. 798. The contents of table 38 — illustrated also by map fig. 115 — regarding the historical groups of the Fennoscandian Carabid fauna (362 species) may be summarized as follows:

Würm-survivors:† 97 ± sure species = 27.1 percent of the fauna.
(In addition 33 "possible" species.)

Southern immigrants: 280 ± sure species = 78.2 percent of the fauna.
(In addition 12 "possible" species.)

Eastern immigrants: 267 ± sure species = 74.6 percent of the fauna.
(In addition 23 "possible" species.)

Only 25.4 percent of the species have a simple origin, belonging to one of the three groups only; 50.3 percent have a double, and no less than 24.3 percent a threefold origin.

An example of how one may imagine in detail the history of a ± panfennoscandian species is given by *Bembidion saxatile* (fig. 116).

The influence of the last glaciation (Würm) on the Fennoscandian fauna and flora may simply be expressed thus: This period has played a decisive rôle in the details of the distribution of species. But the stock of Fennoscandian species was only little changed.

†(= "Würm hibernators"; cf. p. 798; suppl. scient. edit.).

SUPPLEMENT TO PARTS I AND II

In the three years since 1945 an extraordinary number of finds of carabids from new localities in Fennoscandia have been added. However, here I give only finds that enlarge the earlier distribution map or significantly add to it*. Only two species are new for the region: *Lionychus quadrillum* and *Perigona nigriceps*.

There are also numerous important new observations on the ecology, "biology" and dynamics of the species. Also, I had overlooked some observations in the older literature**.

On the other hand, the numerous new fossil records—insofar as they concern Fennoscandia—are not taken into consideration in this Supplement. A synoptic account of them is given above (pp. 656 ff.).

The following abbreviations of authors' names may be added: FRD—Axel Ridén; HLD—Nils Höglund.

Acupalpus consputus. Gtl Fårön, Ekeviken, in drift material, May 9, 1948, 2 specimens (HLD !); Sandön, July 6, 1946, 1 specimen on the shore (JNS !).

In captivity the beetle likes to feed on bread; it has a high predilection for flight, both during sunshine and artificial light (Öld Halltorp, June 1946; cf. p. 256).

A. dorsalis. Hls Bergvik, March 29, April 6, 1945, April 1948 (HLD !). Completely isolated: Vbt Vännäs, July 7, 1944, 2 specimens (SDH !).—Oa Lappfjärd, 1944 (LBH). Ko Jallahti, 1943 (KNG ! KAN !).—Estonia, Ösel (SZL, 1942, p. 184).

Numerous additional records of spontaneous flight, especially in the afternoon sun (PME, 1946, p. 32).

A. dubius. The remarkable record of this species on the small island of Sturkö in Ble dates from April 30, 1947 and May 12, 1948, where it was found

*The old account by Ekström (1828) from the Mörkö parish in Sdm was completely new to me. It lists (pp. 50–51) about 80 species of carabids; the nomenclature and serial arrangement follow Gyllenhal (1810). It is not clear from the text whether the determinations were made by Ekström or were at least checked by an entomologist. However, the list gives the impression of being quite reliable. Only the occurrence of *Carabus convexus* and *Dichirotrichus pubescens* (*"Harpalus p."*) may be doubtful.

**The interesting contribution by H. Krogerus (1948) is not taken into consideration here. It contains precise data on the development periods and migration of riparian carabids. His observations agree with my own data.

in great numbers by Nils Höglund. He gives the following description of the locality: On the northwestern bank of a small, nutrient-rich but also humus-rich pond situated between two stony gravel ridges. *Alnus glutinosa* on hummocks, solitary *Betula* and *Juniperus*. *Sphagnum* in patches, surrounded by firm ground with *Myrtillus*. The insect was found in moist "förna"† under *Alnus* at some distance from the waterside.

A. exiguus. Gtl Fårön, in drift material, June 1946 (Palm). Vrm Visnum-Kil, shore of Lake Väner, May 17, 1946, 1 specimen (WRN !).—Latvia, 2 localities (LCK, 1942, p. 175).

Hibernates as adult, often quite far from the shores (Sv; PME, 1946, p. 32).

844 *A. flavicollis*. Öld Halltorp, *Amblystegium* swamp, June 11, 1946, 1 specimen, June 14, 1947, 1 specimen (LTH). Ögl St Anna. Rödskär, May 26, 1947 (WSJ !). Hls Bergvik, May 21–23, 1947, 8 specimens (HLD ! LBL, RM !).

Striking change of habitat, during winter far from the shores, even on heathland (Sv; PME, 1946, p. 32).—1 specimen observed flying upon exposure to sunlight under glass (Öld Halltorp, June 1946).

A. meridianus. Vrm Kristinehamn, March 27, 1946, numerous specimens (WRN).—Nl Dragsvik, September 21, 1947 (NUM); Hangö, 1946, numerous specimens on cultivated soil (PME).

Numerous immature beetles, July 19 through August 24, 1947 (Skå Hälsingborg, PLQ!).—Both in Latvia (LCK, 1942, p. 175) and in Skå Hälsingborg (March 17, 1947, 5:30 p.m., ♂, PLQ!) spontaneous flight.—According to HNS and LRS (1941, p. 350), probably in captivity also feeds on vegetable diet.

Agonum assimile. Oa Lappfjärd, 1944 (LBH).

In copulation, May 21, 1946 (Skå Hälsingborg, PLQ). Hibernating adults (Sv; PME, 1946, p. 40).

A. bogemanni. Ko Kolatselkä, June 30, 1944, 1 specimen (Tiensuf!).

A. consimile. Jtl Häggenås, July 2, 1944, 1 specimen (KRG!). Lyl, 5 localities in Tärna region, 1945–1948 (FRD!).—Siberia, Yenisei region, Kureika (SBJ 1880, p. 39; MÅ!).

A. dolens. Lyl Tarna region, 4 localities, 1945–1948 (FRD!). Tol Silkimuotka, June 23, 1947, July 1, 1948 (HLD!).—According to HOR (*in litt.*) the report from Slovakia is very doubtful.

Spontaneous flight, Dsl Hästfjorden, May 14, 1944 (FRD!).

A. dorsale. Ögl Mogata, August 1946, numerous specimens (LTH). Sdm Morko (Ekström, 1828, p. 50).

Copulation in captivity, May 21, May 26 (Upl). Fed exclusively with bread for several months; also feeds on fresh pieces of *Lumbricus* and on all kinds of dead insects, but does not attack any living animal.—After many unsuccessful experiments, 1 ♀, June 25, 1947 (Öld Greby), flew repeatedly upon exposure to artificial light.

†(= "upper litter layer of the soil profile"; suppl. scient. edit.).

A. ericeti. Upl and Gst, 3 localities in the lower Dalälv region, 1945 (ELS!). Dlr Grövel Lake, July 6, 1944, 1 specimen (FRD). Jtl Häggenås, Storflon, August 8, 1945 (Palm!). Lyl Umgransele, 1947, 1 specimen (B. Persson!).—HOR (*in litt.*) believes the rècord from northern Spain is doubtful.

Copulation in captivity, May 16, and larvae at the end of first instar, June 3, 1947 (Sdm Ricksten, LTH). The beetles fed on bread and a crushed geometrid larva; a living one was not attacked.—In Austria (Kärnten, Kosmatica) spontaneously flying individuals were seen, June 18, 1939 Hölzel, according to HOR, *in litt.*). The species thus shows wing dimorphism.

A. gracile. Tol Nedre-Soppero, June 4, 1948, 1 specimen (HLD!).

One specimen spontaneously flying during sunshine (around 1300 hours), (Upl Ängby, Rocksta Lake, May 26, 1946).—Under "fossil records" Skåne should be included instead of Denmark.

A. gracilipes. Hll Harplinge, 1 specimen (FGQ, RM!). Öld Greby-Alvar[†] (for locality, see Fig. 11, p. 117), June 14, 1946, 1 specimen (LTH).—Al Kökar, Idö, seashore, June 1947, 4 specimens (STK, STN!).

A. impressum. Hibernating adults observed in November (Sv; PME, 1946, p. 40).

845 *A. krynicki*. Copulation observed in captivity, July 3; likes to feed on bread (Öld Halltorp, 1946).

A. livens. Vrm Visnum-Kil, May 4, 1947 (WRN!).—2 new localities in central Jutland (West, 1947, p. 17).

Numerous immature beetles, September 30 (Denmark; West, l.c.), 1 specimen also on May 4, 1947 (Vrm, WRN!).

A. lugens. Bornholm (West, 1947, p. 17).—Latvia, Papenhof, repeatedly recorded (LCK, 1942, p. 174).

Likes to feed on bread, but when offered a fresh piece of *Lumbricus*, the beetle immediately leaves the bread; also cannibalistic on killed conspecific specimens (Upl).

A. mannerheimi. Latvia, Tauerkaln, July 15, 1938, 1 specimen (LCK, 1942, p. 174).

A. marginatum. In Mecklenburg under moss, together with *Chlaenius tristis*, hibernating at least 2.5 km distant from the water (NBG, *in litt.*).

A. micans. Tb Pihlajavesi, 1944, 1 specimen (PHJ!). Sv. Kuujärvi and Ulvana, 1943 (KNG! KAN!).—? Ösel, 1937 (SZL, 1942, p. 185; "*scitulus*").

Immature beetle, September 4, 1946 (Jtl, Ragunda, Palm!).—Spontaneous flight (Upl Danderyd, Nora, May 13, 1945, LTH).

A. moestum. Hls Tönnebro, May 26, 1947, 1 specimen (HLD!).—Kø Teru, June 6, 1943, 1 specimen (HLL!).—[Boh Öckerö is to be excluded; the record from this locality pertains to *viduum*!].

[†](cf. p. 118; suppl. scient. edit.).

Several immature beetles, August 23, 1946 (Upl Lovön). Spontaneous flight (Upl Danderyd, Nora, May 13, 1945, LTH).

A. mülleri. Small larvae in early June (Denmark; West, 1947, p. 16).—Spontaneous flight (Dsl Hästfjorden, May 8, 1944, FRD).

A. munsteri. Dlr Lima. Östra-Kullstjärn, *Sphagnum* quaking land, July 21, 1948, 2 specimens (OLS!). Jtl Revsund, July 16, 1944, 1 specimen (BGW!); Häggenås, Storflon, August 8, 1945, several specimens (Palm!). Nbt Kihlangi, *Sphagnum* quaking land at forest lake, June 1947, numerous specimens (Palm!).

According to KRG (*in litt.*) markedly acidophilic.—Immature beetles, August 11, 1945 (Nl Hangö, Täcktom; THG!).

A. obscurum. Upl Fogdö, 1948, several specimens (KLF). Isolated localities: Hls Skog, Södra-Brännigen, April 11, 1945, 4 brachypterous specimens (HLD!).—Ösel (SZL, 1942, p. 185).—Calabria (SZM, *Rivista Sc. Nat. "Natura"*, 34, Milano, 1943, p. 94).

Spontaneous copulation, July 19, 1945 (Skå Visseltofta, PLQ). Numerous immature beetles, July 16; hibernating adults observed (Sv; PME, 1946, p. 41).

A. piceum. Ble Karlskrona, April 7, 1946 (SDH!). Lyl Lycksele, Yttre-Stenträsk, September 8, 1946 (FRL!). Nbt Kihlangi, June 1947, 1 specimen (Palm!).—Kc Ontrosenvaara, May 1944. Tiiksa, May 1943 (Laamanen!).

In Mecklenburg hibernating under moss, 2.5 km distant from the water (NBG, *in litt.*).

A. quadripunctatum. Kl Valama (Y. Kangas).

Near Lyl Umgransele found repeatedly and in great numbers, but exclusively at fresh charcoal kilns (B. Persson, *in litt.*). In Sv in large numbers on sandy and loamy shores (PME, 1946, p. 39); which could be (?) its primary biotope. In Mk Brandenburg (in 1947) it suddenly appeared in hundreds at a freshly burned location, and also in a house where linseed oil was being carbonized; had not been recorded since 1880 (WGN, *in litt.*).

Immature beetles, August 3 (Ko Säntämä) and August 9 (Ko Vitele), 1943, (KNG!). Several hibernating beetles in a pine trunk, November 28 (Sv; PME, 1946, p. 39).

A. ruficorne. Several immature beetles, August 10, 1946 (Ögl Mogata).—In captivity the beetle feeds on bread and crushed flies (Ögl Mogata).

846 *A. sexpunctatum*. Upl Singö, July 16, 1948, 1 specimen on the seashore (KLF). Dlr Älvdalen, Mjågen, August 30, 1944 (SVS). Ång Kyrktå Lake, 1946 (R. Jonzon, coll. GTZ!). Lyl Tärna, Rönnbäck and Gejmån, June 1948, 8 specimens (FRD). Tol Nedre-Soppero, June 3, 1948, 1 specimen (HLD!); Karesuando, June 1947 (Palm).

Copulation in captivity, June 15, 1947 (Öld Hornsjön).—The beetle fed on bread, crushed flies and an uninjured elaterid pupa (Ögl).

A. thoreyi. Gtl Sandön, June 30, 1947, 1 specimen (WRN!). Hls Bergvik, March 24, 1945, May 23, 1947 (HLD! LBL, RM!).—Kl Valamo (J. Kan-

gas!). Sa Mäntyharju (THG, MH!). Sb Kuopio, June 1945, about 10 specimens (ELF).—The three northernmost localities (32 Salten; Lk Muonio; 41 Vaggatem) are to be excluded as doubtful.

According to KRG (*in litt.*) very alkalophilic.—Spontaneous flight, Gtl Sandön, June 30, 1947 (WRN!); attracted to light in Hungary (Dorn, 1946).

A. versutum. Kc Novinka, May 18, 1943 (Laamanen!).

Several spontaneously flying individuals observed (Öld, Upl).

A. viduum. Impelled to fly upon exposure to sun under glass (Ab Lojo, July 1945, KRH; Upl Ängby, May 1946, LTH).

Amara aenea. Vrm Östmark, Rännberg, August 6, 1935 (R. Broberg). Hls Ramsjö, 1943 (LDN).

Spontaneous flight: Skå Åkarp, May 9, 1947, in sunshine, 3:30 p.m. (CHR); Upl Ängby, May 26, 1946, 2 specimens, about 1:00 p.m. (LTH); England (E.M.M., 83, 1947, p. 245).

A. alpina. Distribution map also by HNR (1933, p. 297).

In Lyl Tärna region up to 1524 msl† (also one pupa), 1945 (FRD).—5 specimens in drift material along Torne-träsk, July 1948 (Palm).

A. apricaria. Gtl Sandön (JNS, 2 specimens RM! MJB, 4 specimens, VA!), 1947, 3 specimens (WRN!).

In Sv, numerous immature beetles from August through mid-September (PME, 1946, p. 35). Spontaneous copulation, August 20, 1948 (Hll Harplinge).—Numerous observations of spontaneous flight (Ble, Små, Upl, Vrm).

A. aulica. Lyl Tärna region, several localities, 1945, 1946 (FRD).—Ösel (SZL, 1942, p. 184).—Calabria (SZM, *Atti Soc. Ital. Sci. Nat.*, 80, 1941, p. 61).

Immature beetles in June and September (Sv; PME, 1946, p. 36). Observed spontaneous feeding on a crushed *Harpalus pubescens* (Ögl Mogata, August 12, 1946).—Flying to light near Warsaw, 1947 (MAK, *in litt.*).

A. bifrons. Tol Abisko, railroad embankment, September 10, 1947, 1 specimen (SJB, coll. LTH).—Om Brahestad, 1944 (LBÅ).—Kc Ontrosenvaara, September 1943, 2 specimens (Laamanen!).

Caught by OSS (!) at three localities (Skå, Små, Upl) in a flight trap; undoubtedly came flying.

A. brunnea. 8 Gloppen, Skjerdal, August 1946 (WSJ!).—Ob Rovaniemi (Y. Kangas!).

Lyl Tärna, Morts mountain, 1 specimen from heathland, 1300 msl (July 12, 1945, FRD!); also in northern Norway in the *Regio alpina*, (STA, 1946, p. 105).—Immature beetle in August (Sv; PME, 1946, p. 35).—Numerous specimens in drift material on the shore of Torne Lake, July 1948 (Palm).

A. communis. Nbt Kihlangi, June 1947 (Palm).—Ösel (SZL, 1942, p. 184).

1 specimen spontaneously flying during sunshine, Upl Ängby, May 26, 1946, about 1:00 p.m.

†(= "above sea level"; suppl. scient. edit.).

According to personal communication from J. Makolski, Warsaw, and K. Kult, Prague, *communis* s. l. (including *convexior* Steph.) comprises three separate species. I am undecided on this question.

A. consularis. Immature beetles, June 15 (Öld Vickleby, 1946, WRN!), July
847 24, August 10 (Sv; PME, 1946, p. 36).—Spontaneous flight in the evening: Små Skirö, July 8, 1945 (BRC!), Sb Vehmersalmi, July 1946 (HDL).

A. convexiuscula. Skå Ven, May 24, 1946 (LLR!). Gtl Rone, Ytterholmen, April 26, 1946, 3 specimens (HLD!).

Reports on flight (not taken into consideration above) from Holland (*Ent. Berichten*, 12, 1949, p. 341).

A. crenata. Near Erlangen, in autumn and spring, abundant on open, dry, loamy soil; succeeding species, among others *Brachynus* (probably *explodens* Dft.) (Rosenhauer, S. E. Z., 32, 1871).

A. crusitans. Ta P.-Pirkkala (Y. Kangas! GBL, coll. HDL!).

A. curta. Hls Bergvik, May 23, 1947, 1 specimen (LBL, RM!).

A. equestris. Hls Los, June 15, 1946; Ljusdal, September 17, 1947 (SJB).—I had overlooked the record from Bornholm (West, 1941, p. 632; 1947, p. 15).

Immature beetle, July 2, 1946 (Öld Halltorp, WRN!). Pupation on June 3, emergence on June 22 (Denmark; West, 1947, p. 15).—Fed in captivity on bread and crushed flies (Ögl Mogata, August 1946).

A. erratica. Lyl Skalmodal, Potato field, June 26, 1947, 1 specimen (FRD!). 1 specimen in drift material at Torne Lake, July 1948, (Palm).

A. eurynota. Kc Ontrosenvaara, September 1943, 3 specimens (Laamanen!).

A. femalica. Vgl Fristad, Skalle, May 20, 1944, 1 specimen (SVS!).—Oa Lappfjärd, 1944, several specimens (LBH!). Om Lappi, August 13, 1944, 1 specimen (LBÅ!). Siberia, Tobol (BGR, MH, as "*erratica*"!).

A. familiaris. 32 Mo in Rana, July 29, 1945 (FRD).—Lyl, Tärna region, 2 localities, several specimens, 1946 (FRD!). Tol Paitasjärvi, June 16, 1947, 1 specimen (HLD!); Abisko, shore of Torne Lake, 1947, 1 specimen (Palm!).—Li Ivalo, July 8, 1939, 1 specimen (THG, coll. PME!).

A. fulva. In Sv, immature beetles, August 29, September 5 (PME, 1946, p. 35).—2 specimens spontaneously flying during bright sunshine. June 20, 1945, Vgl Brandstorp (C. Thorén).

A. fusca. Skå Hälsingborg, Raus-marker, September 8, 1946, October 5, 1947 (PLQ!).—3 new localities (Sjaelland, Falster) in Denmark (West, 1941, p. 632; 1947, p. 15).

A. infima. Öld Stora-Rör, numerous specimens under *Calluna* on sand, June 1946, June 1947 (LTH).

A. ingenua. The records from Vbt Umeå (GTZ) are from 1908 and 1909. Lyl Umgransele, July 18, 1946 (B. Persson!).—Al Eckerö, Torp, 1943, 1 specimen (LBÅ)—Kc Ontrosenvaara, September 1943, 6 specimens (Laamanen!).

In captivity fed exclusively with bread for several months (cf. also p. 539); also feeds on dead conspecific specimens.

A. interstitialis. In Sv, near Ladoga, strangely a fairly pronounced riparian species (PME, 1946, p. 34). 1 specimen on heathland, 1358 msl (probably got lost in flight), near Lyl Tärna, Dalåve (July 19, 1945, FRD!).

A. littorea. Öld Borgholm, July 9, 1945, 1 specimen (ARV!). Jtl Oviken, 1948, 1 specimen (H. Nyblom through KLF!).—Ok Ruhtinassalmi (SSK, coll. STK!).—Austria, Leitha mountains, 1 specimen, Zurndorf village, 2 specimens (Franz, *in litt.*).

A. lucida. Gtl Sandön (JNS, RM, as *tibialis*!), June 22, 1947, 1 specimen (WRN!).

In captivity likes to feed on bread.

A. lunicollis. Lyl, Tärna region, 2 localities, 1945, 1946 (FRD!). Tol Karesuando, June 1947, 3 specimens (Palm!).—Lk Pallastunturi (RNK, coll. KNG!).—Calabria, 1 specimen (SZM, *Atti Soc. Ital. Sci. Nat.*, 80, 1941, p. 60).

1 specimen in the lower *Regio alpina* (790 msl) near Lyl Tärna, Laxfjäll, June 25, 1945 (FRD!).—1 specimen observed flying up on exposure to sun in glass (Upl Djursholm, April 4, 1945).

848 *A. majuscula.* In recent years a large number of localities have been added, illustrating the advancing propagation of the species. Ble Sjöarp, 1945 (HEQ!). Hll Östra-Karup, 1944 (SJB!); Harplinge, Särdal, 1948 (LTH). Små Vimmerby, 1944 (LLR!). Öld Byerum, 1937 (HNS, coll. LDN!). Gtl Visby, 1945 (LTH). Nke, Örebro, Oset, 1941 (JNS!); Mullhyttemo, 1944 (LLR). Upl Älvkarleby, Långsand, 1944 (WSJ!). Hls Bergvik, 1945 (HLD!).—Ab Jurmo, 1947 (Linnavuori!). Ka Tytärsaari, 1938 (HLL, MH!); Seiskari, 1938 (THG, coll. PME!). Kl Parikkala, 1945 (HLL!). Ta Längelmäki, 1943 (Kontuniemi!). Sb Vehmersalmi, 1943, 1944 (HDL!).—Poland, among others Warsaw (MAK!).

PME's opinion (1946, p. 35) that the species is hygrophilous cannot be correct.—Some immature beetles in June 1947 (Al Kökar, Idö, STK).—Flying to light in the evening (in some cases in large numbers) in July and August, from 7:27 p.m. onward (Warsaw, MAK, *in litt.*). 1 specimen caught by OSS (Upl Solna, August 1947!) in flight trap.

A. montivaga. Dlr Siljansnäs, Björkberget, May 30, 1948, 1 specimen (KLF); Rättvik, June 23, 1945, 1 specimen (Bernell, coll. ARV!), May 30, 1946 (TJT!).—Ta Forssa, 1940 (Kontuniemi!).

A. municipalis. Lyl Tärnaby, oats field, May 25, 1946, 1 specimen (FRD!). June 23, 1947 (Öld Greby Alvar)[†] several specimens, all immature.—1 specimen in flight trap, caught by OSS (September 1947, Upl Solna!).

[†](Plant community consisting typically of mosses and calciphilous herbaceous plants that grow on steppelike shallow alkaline soils overlying Scandinavian limestones; suppl. scient. edit.).

A. nigricornis. Siberia, Shigansk on the Lena (PPP, "*erratica*" MH!, 1 ♀ with light brown-red first antennal segment); Irkutsk (leg. ?, ♂, coll. Kult!).

A. nitida. Dlr Rättvik, June 24, 1945 (Bernell, coll. ARV!). Kn Ahvenjärvi, 3 specimens (THG, MH!).

A. ovata. Ögl St Anna, Stickelskär, July 18, 1946 (WSJ!).—Al Eckerö, Torp, 1943, 1 specimen (LBÅ).

Observed flying upon exposure to sunlight, June 14, 1945, ♂; spontaneous flight, May 23, 1947, ♀ (Upl Djursholm); also May 21, 1947, ♂♀ (Hls, Bergvik, HLD!).

A. peregrina. The record from Lt Kola is incorrect (MH = *alpina*!).

A. plebeja. Lyl Tärna region, 1947–48, 2 localities, 3 specimens, (FRD).—Kb Valtimo (Y. Kangas!).

Several reports of spontaneous flight (Små, Vgl, Upl, Dlr; Sb).

A. praetermissa. Ab Korpo, August 7, 1943 (WLG). Nl Pärnå, August 8, 1940 (Kontuniemi!).

Repeated copulation observed in captivity, August 24 through September 5, 1946 (Upl Djursholm).—1 ♀ observed flying upon exposure to sun in glass (June 24, 1946, Upl Djursholm).

A. quenseli. Dlr Falun, Österå, May 7, 1944, 1 specimen (KLF!).—Ko Jallahti (Jalguba), June 13, 1943, several specimens (KNG! KAN!). Kc Ontrosenvaara, September 1943, 6 specimens (Laamanen!). Solovetsk, Anserek (LEV, MH!).

Immature beetle, June 13 (Ko Jallahti, KNG!).—3 specimens in drift material on Torne Lake, July 1948 (Palm).

A. similata Lyl Umgransele, May 9, 1948. 1 specimen (B. Persson!).—Ok Ruhtinassalmi (SSK, coll. J. Kangas!).

2 immature beetles, August 13 (Sv; PME, 1946, p. 33).—Spontaneous flight: Upl Danderyd Nora, May 13, 1945; Ängby, May 26, 1946 (LTH); Ång Undrom, June 1947 (OSS!).

A. tibialis. Vbt Hällnäs, June 7, 1946 (HEQ!).

Spontaneous flight in the evening, Sb Vehmersalmi, July 1946 (HDL).

A. torrida. Lyl Umasjö, 520 msl, August 5, 1945, 1 specimen; Vapstdalen Gränsjärvi, *Regio betulina* (570 msl), June 9, 1946, 1 specimen (FRD!).

849 In Norway never found above the timberline (STA, 1946, p. 107).—1 specimen in drift material on Torne Lake, July 1948 (Palm).

Anisodactylus binotatus. Skå Sandhammaren, Hagestad-mosse, June 24, 1947 (WSJ!). Dlr Svärdsjö, Hillersboda, July 23, 1944 (Dubois, according to KLF); Älvdalen, Mjågen, August 30, 1944 (SVS). Hls Bergvik, April 6, 1945, 2 specimens (HLD!).—Sb Vehmersalmi, July 13, 1944, 1 specimen (HDL).

Spontaneous flight observed 3 times (Sdm, Upl).

A. nemorivagus. Sv Kuujärvi, July 29, 1943, 1 specimen (KNG!); Uslanka, July 25, 1943, 1 specimen (PME, 1946, p. 33).—In Sjaelland 2 instead of 3 localities (West, 1941, p. 632).

Asaphidion flavipes. Gtl Sandön, July 1946, (JNS).

According to PME (1946, p. 23) in eastern Karelia the species shows a distinct change of habitat in that it stays constantly on the shore only in early summer and is far more eurytopic in spring and late summer until autumn.

A. pallipes. The Swedish "mo" instead of "mjäla" should be used for the ground material.

Badister bipustulatus. Harald Lindberg has shown that the form occurring on the Finnish mainland is different from the *forma typica* occurring in Åland and in Scandinavia, and is apparently identical with *B. lacertosus* Sturm. The most important differences according to him (*in litt.*)* are: Larger body size (6.5–7.2 as against 5.5–6.4 mm); more iridescent elytra because of closer and more regular granulation ("Chagrinierung")[†]; large, black elytral spot transversely divided in front; pale scutellum; first antennal segment more or less darkened at the apex; pale hind tarsi. Besides, the tip of the penis is said to be more slender, without excavation of the dorsal margin at the extreme apex (as in *B. bipustulatus* s. str.; visible laterally). An examination of most of the Swedish material showed that *B. lacertosus* also occurs in our region and has a characteristic eastern distribution (Fig. 117), but one of the above-mentioned characteristics was found to be completely consistent, not even the structure of the penis. Adding up the characteristics, it is of course always possible to decide whether an individual should or should not be assigned to *B. lacertosus*; however, in 1 to 3 of the above-mentioned 6 characters it may be completely identical with *B. bipustulatus* s. str. *B. lacertosus* certainly has a completely independent history of immigration. But it is not possible to grant it a higher status than that of a subspecies, especially since the externally similar *B. unipustulatus* has a very different internal structure of the penis (Lindroth, 1943b, p. 18), whereas this seems to be identical in *B. lacertosus* and *B. bipustulatus* s. str. Since even the Finnish material of *B. lacertosus* shows considerable variability, it is uncertain whether the low constancy of characters could have arisen through hybridization. On the other hand it is clear that *B. lacertosus* is most variable in southern Sweden (up to Ögl). The relatively greater homogeneity (for instance, in the form of the dark elytral spot) may indicate that the more northern Swedish stock immigrated directly from Finland.

It was not possible to examine the entire Swedish material of "*B. bipustulatus* s. l.". However, if the map in Part II holds good for *B. bipustulatus* s. str., at least the following localities must be excluded: all localities on the Finnish mainland; all Swedish localities north of the River Dalälven (Dlr, Gst, Hls); Gtl Sandön; Vgl Tived. The northernmost definite record of *B. bipustulatus* s. str. in Sweden is Upl Älvkarleö, June 27, 1936 (LTH). In Norway only
851 the *forma typica* seems to exist (on the basis of 50 specimens in MO!). The

*In the meantime this has been published: *Notulae Ent.,* 28, 1949, pp. 96 ff.

[†](suppl. scient. edit.).

subspecies *B. lacertosus* also occurs in Denmark; I have examined 1 ♂ from Falster, Korselitse, June 1, 1936 (HSN); according to West (*in litt.*) also found in Sjælland and Lolland.

The subspecies *B. lacertosus* seems to be more hygrophilous.—Immature beetle (*forma typica*), September 16, 1931 (Stockholm, SJB!).

B. dilatatus. Små Öster-Korsberga, Hjärtasjön, December 28, 1926 (GTZ!). Gtl Källunge and Hammarsänget in Lärbro, June 1946 (Palm); Fårön, Ekeviken, drift material, May 9, 1948, 1 specimen (HLD!); Sandön, seashore, July 4, 1946, 2 specimens (JNS!).

Copulation in glass, June 16, 1947 (Öld Halltorp). Numerous individuals fly in the evening upon exposure to sun, June 1946, June 1947 (Öld Halltorp).

Badister peltatus. Ab Korpo, June 1946, 1 specimen (WEG!)*. Sb Kuopio, June 1947, 9 specimens (ELF).—Ösel (SZL, 1942, p. 183).

Several specimens fly in the evening upon exposure to sun, June 1947 (Öld Halltorp).

B. sodalis. Upl Ekolsund, April 20, 1947, 1 specimen (WSJ, coll. LTH).—Ko Petrozawodsk, at brookside in *Aconitum* grove, April 23, April 29, 1944, 2 specimens (KRV).—Ösel (SZL, 1942, p. 183). Latvia, Alt-Autz, April 19, 1939, 1 specimen (LCK, 1942, p. 175).

B. unipustulatus. Ka Hogland, 1 specimen (SRS, MH!); Koivisto, Vasikkasaari, July 10, 1939, 1 specimen (KNG!).

In captivity feeding on a crushed fly (Öld Halltorp).—Numerous specimens fly in a glass upon exposure to sun (Upl Ängby, May 1946; Öld Halltorp, June 1947).

Bembidion aeneum. In captivity readily feeding on bread (Boh Sämstad, August 1946).—Several specimens fly upon exposure to artificial light (Öld Möckelmossen, June 1947).

B. andreae polonicum. Gtl Fårön, 1901, 2 specimens (O. Lindbom!).

Immature beetle, August 12 (Sv; PME, 1946, p. 26).

B. articulatum. Ble Jämjö, Färsksjön, July 28, 1945 (SDH!).—Ka Miehikkälä and Virolahti, 1940 (PFF, coll. PME!).

According to PME (1946, p. 27) the species shows a clear change of habitat in eastern Karelia and was observed hibernating under bark of trees quite distant from the shore.—Spontaneous flight in sunshine (Upl Adelsö, May 25, 1947).

B. assimile. Al Finström, 1943, (LBÅ). Nl Ekenäs, Jussarö, 1946 (PME).—Ösel (SZL, 1942, p. 183).

B. azurescens. Ösel (SZL, 1942, p. 183, "*tenellum*").

In Sv partly in May, partly September (PME, 1946, p. 26).

B. biguttatum. Spontaneous flight observed in England too (E. M. M., 83, 1947, p. 244).

*This record was not included while discussing the fauna of the islands.

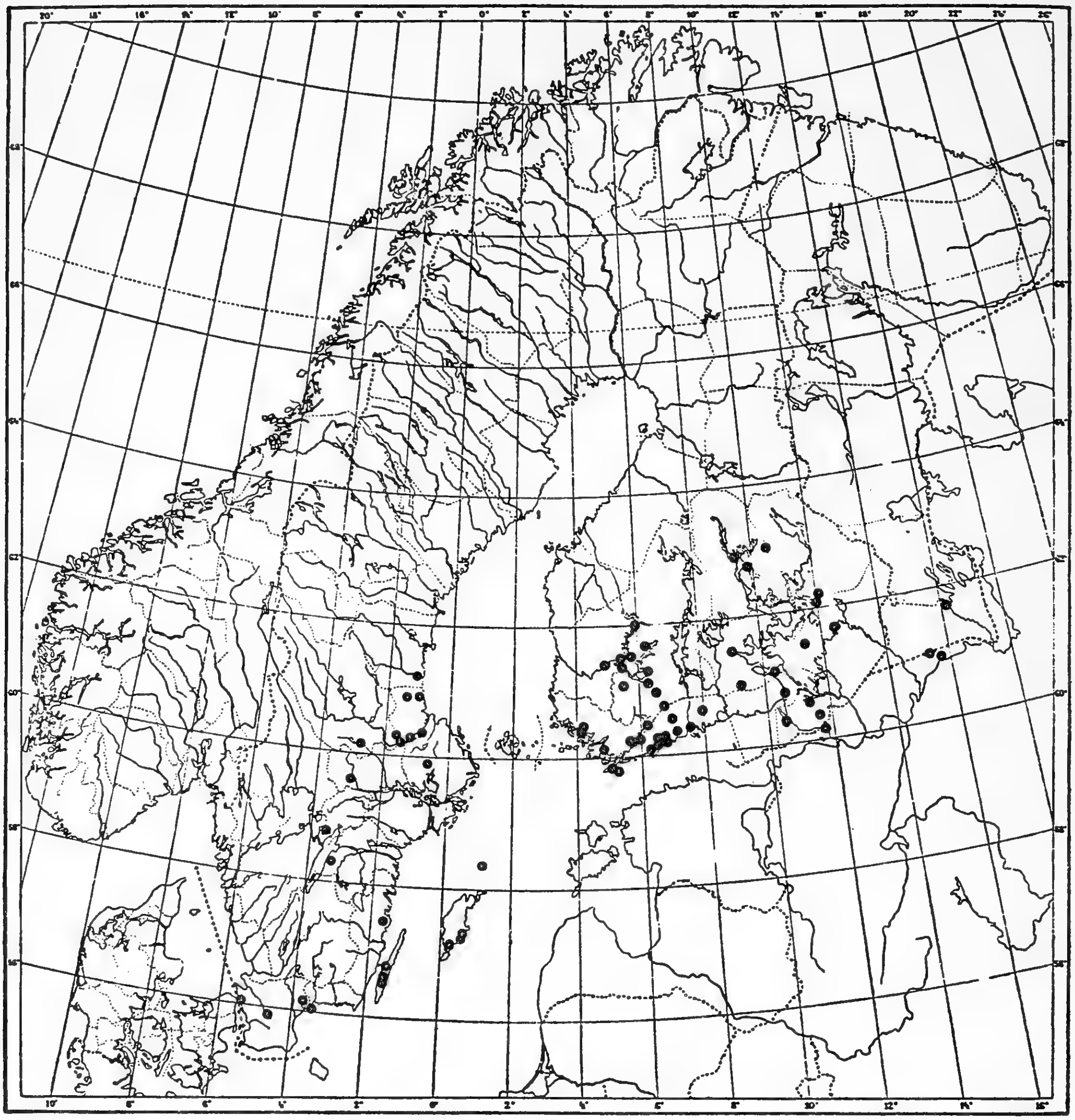

Fig. 117. *Badister bipustulatus lacertosus* Sturm. Preliminary map.

B. bipunctatum. Hibernating beeltes observed in pine stumps on a heath (Sv; PME, 1946, p. 24).—Immature beetles, August 14, August 23 (Sv; PME, l.c.). Spontaneous flight: Dsl Frändefors, May 14, 1944 (FRD).

B. 'dauricum. Lul Virihaure, *Regio betulina* and lower *Regio alpina* (to 850 msl), July 1944, 8 specimens (BRK!).—Lk Pallastunturi, July 12, 1938, 1 specimen together with *Bledius lativentris* Janss. (KNG!) and others.

On Lake Virihaure (Lul) on dry, heathlike ground with *Empetrum*, *Betula nana*, and the like, mostly together with *Miscodera* and *Hypnoides rivularius* Gyll. (BRK).

852 *B. dentellum*. Oa Kauhajoki, August 15, 1939 (KNG!). Kb Jukka, June 30, 1940, 2 specimens (KRG!).—In northeastern Russia at least as far as Archangel (ENW, 2 specimens MH!).

B. difficile. Vbt Hällnäs, July 30, 1947, 2 specimens (HEQ!). Lyl Tärna region, several localities, 1945, 1946 (FRD!).

B. doris. Nbt Kihlangi, June 1947 (Palm).

The species shows clear change of habitat in Sv and stays on the shore only from mid-May through early September (PME, 1946, p. 27).—Immature beetle, August 18 (Sv; PME, l.c.).

B. fellmanni. Tol Karesuando, June 1947 (Palm).—19 Jostedal, September 1946 (Jan Lindroth!).—Kanin Peninsula (PPP, 1909, 2 ♀, MH!). Siberia, Yenisei region, on the islands Nikandrovsk (♂) and Briokovsk (♀) (SBJ, 1880, p. 20; MÅ!).

Immature beetles, September 8, 1947 (Tol Abisko, SJB).

B. femoratum. Skå Ivön, June 1946 (LBL, RM!). Gtl Sandön, June 21, 1947, 1 specimen (WRN!). Upl Forsmark, 1946 (SJB).—Ko Vitele, 4 specimens (J. Kangas!).

B. fumigatum. Skå Lomma, April 4, 1943, 1 specimen (NYH, O. E., 1945, p. 153), June 3, 1947, 1 specimen (JNS). Hll Harplinge, Särdal, 1 specimen in a small spring fen on sand about 100 m from the sea, August 18, 1948 (LTH).

B. gilvipes. Hls Bergvik, 1945, 1946, numerous specimens (HLD!).—Oa Lappfjärd, 1944 (LBH).—Sv, 4 localities (PME, 1946, p. 26).

B. grapei. Dlr Orsa, Fryksås, June 9, 1937 (TJB!). Hjd Tänn valley, July 14, 1944 (FRD!). Lyl Umgransele (B. Persson!); Tärna region, 4 localities, 1945, 1946, numerous specimens (FRD!).—Lt Palaguba (PPP, 1905, p. 90; earlier not identified on the map; situated at the mouth of the Kola fjord).

B. grapeioides. Near Tol Björkliden, 13 specimens in fissures of flushed soil on moraine ground; succeeding species are *Bledius lativentris* Janss., *Bembidion fellmanni*, *Hypnoidus algidus* J. Sahlb. (Palm!).

B. guttula. Hls Bergvik, 1945, numerous specimens (HLD!). Jtl Ås, June 1947, 1 specimen in flight trap (OSS!).—Oa Lappfjärd, 1944 (LBH).—Ösel (SZL, 1942, p. 183).—North Africa (SZM, *Atti Soc. Ital. Sci. Nat.*, 80, 1941, p. 56).

Several observations of spontaneous flight (Upl, Jtl).

B. harpaloides. HOR (*in litt.*) thinks it has no association with animal nests. He repeatedly found many specimens of the species (in Germany) under bark and in cracks of damp decaying branches (especially of *Salix*) lying on the shore of a large pond.

B. hasti. Lyl Tärna region, several localities (440–840 msl), 1945, 1946 (FRD!).

B. hirmocoelum. In Sv, in July and August (PME, 1946, p. 25).—Spontaneous flight near Sv Vaaseni (KRV, S. H. A., 1945, p. 51).

B. humerale. Al Eckerö, 1943, 1 specimen (LBÅ).—Ko Petrosavodsk, lakeside, June 11, 1944 (KRV).

B. hyperboraeorum. Lyl Tärna region, 4 localities (460–670 msl, i.e. right up to the timberline, 1945, 1946, several specimens (FRD!). Lul Virihaure, *Regio betulina* and lower *Regio alpina* (up to 740 msl), July 1944, several specimens (BRK!). Tol Måljotjokk, *Regio betulina*, June 1946, 1 specimen (HLD!).—Siberia, Tolstoinos (SBJ, *"virens,"* MÅ!).

Several immature beetles, August 17, 1945 (Lyl Tärna, FRD!).

B. illgeri. Ösel (SZL, 1942, p. 183).

Immature beetles, August 3, 1946 (Ögl Mogata).

B. lampros. Hjd Tänndalsjon, *Regio betulina* (725 msl), July 11, 1944, 1 specimen (FRD!). Lyl Tärna region, several localities and numerous specimens, 1946, 1947 (FRD!).—Kc Rukajärvi Lake, 1942, Tiiksa, 1943 (Laamanen!).—North Africa (SZM, *Atti Soc. Ital. Sci. Nat.*, 80, 1941, p. 54).

853 3 specimens observed feeding on a fresh, dead *Cephus pallipes* Klg. (Skå Hälsingborg, June 23, 1946, PLQ!).

B. lapponicum. Tol Salamasjärvi, 5 specimens, Måljotjokk, 4 specimens, June 1948 (HLD!).—30 Unkervatn, July 2, 1947, 3 specimens (FRD!).—The dot in the map next to Enare Lake has to be deleted.

B. litorale. Vrm Östmark, Rännberg, shore of Röjdälver, July 1, 1935 (R. Broberg).—"Korkeakoski" is situated in the parish of Juupajoki (Ta) and not in Sb.—Ko Jallahti (Jalguba), 1943, 7 specimens (KNG! KAN!). Kn Karhumäki, June 1943 (PRT!).—Jutland, Nørre Aa (West, 1947, p. 10).

B. lunulatum. Spontaneous flight near Skå Lomma (May, 1947, LDN), in Czechoslovakia 3 times (Kult, *in litt.*).

B. minimum. Gtl Fårön, Ava, sea drift, June 1946 (Palm!); Sandön on the sea, July 7, 1946, 1 specimen (JNS!). Sdm Vagnhärad, Stensund, June 5, 1944, 2 specimens (Matthiessen!).—Oa Kristinestad, 1944 (LBÅ).

Readily feeding on bread (Boh, August 1946). Numerous specimens fly in captivity during artificial light (Boh Sämstad, August 1946).

B. monticola. Sv Mättäinen, May 14, 1944, 1 specimen (J. Kangas!).

B. nigricorne. Nl Lappvik, 1946, 1 specimen (PME). The record from Ik Terijoki is based on a misunderstanding and has to be ignored.—Sv Nurmoila, September 9, 1942, 2 specimens (PME, 1946, p. 24); Aunuksenlinna, July 25, 1943, 1 specimen (KNG!); Ulvana, July 25, 1943, 1 specimen (KAN!).

Immature beetle, August 13 (Kn Karhumäki, 1943, RNK!).

B. nitidulum. Skå Ivö, kaolin pit, September 1945 (NYH). Jtl Åre, July 1944 (KRG). Lyl Skalmodal, at brookside on southern slope, 650 msl, *Regio betulina*, June 26, 1947, 2 specimens (FRD!).

Numerous immature beetles, August 18 (Sv; PME, 1946, p. 25).

B. obliquum. Lyl Umgransele, July 8, 1948, 1 specimen (B. Persson!).—Immature beetles, August 23 (Sv; PME, 1946, p. 25).

B. obtusum. Små Ölvingstorp, September 1947, 1 specimen in flight trap (OSS!); Västervik, September 1947, 1 specimen, collected likewise (OSS!). Öld Vickleby, July 11, 1935, 1 specimen (SJB!); Resmo, April 18, 1946, 2 specimens (WRN!). Gtl Fårön, Ava, sea drift, June 1946 (Palm!).—In southeastern Sweden the species has recently expanded its area: The first definite record from Öld dates to 1930 (the report by BOH is unsupported by record material); known from Gtl since 1926.

The two specimens from Små Ölvingstorp and Vastervik (above) are to be considered as evidence of flight. Spontaneous flight, Boh Lycke, September 16, 1947, in daytime (O. Pehrsson!).

B. octomaculatum. Gtl Fårön, Sudersand, July 1, 1946, 1 specimen on the seashore (JNS!).

In Moravia spontaneous flight was repeatedly observed (Kult, *in litt.*).

B. prasinum. Upl Älvkarleby, shore of Dal River, July, August, 1945, several specimens (ELS!). Mdp Indalsliden, Järkvitsle, August 1, 1945, 4 specimens (LBL, RM!).

B. properans. Gtl Fåron, Ava, sea drift, June 1946 (Palm).—Oa Lappfjärd, 1944, several specimens (Laamanen!).—Kc Ontrosenvaara, 1943, 1 specimen (Laamanen!).—Siberia, Ust-Kut on the Lena (PPP, MH!).

B. punctulatum. Kn Karhumäki, June 1943 (PRT!).

Immature beetle, August 19 (Sv; PME, 1946, p. 24).

B. quadrimaculatum. Ång Kyrktåsjo, 1946 (R. Jonzon, coll. GTZ!). Lyl Umgranselc, in garden, June 13, 1947 (B. Persson!). Lul Gällivare, July 3,
854 1944, 2 specimens (HJG!). Tol Nedre-Soppero, July 1, 1948, several specimens (HLD!); Karesuando, June 1947 (Palm).—Ab Korpo, 1945 (WEG).

Several records of spontaneous flight (Skå, Upl, Jtl; Sb).

B. quinquestriatum. Bornholm (West, 1947, p. 11).

B. ruficolle. Nl Kallvik, 1945 (PRT).—Latvia, Halswigshof, 1939, 2 specimens (LCK, 1942, p. 173).

B. saxatile. Skå Kåseberga, June 26, 1947, 1 specimen (WSJ!). Lyl Tärna, 5 localities (< 554 msl, up to lower *Regio betulina*), 1945 (FRD). Lul Kuouka, July 7, 1948, 2 specimens (HLD!).—Ab Nystad (HLL, coll. PME!).—Kn Karhumäki, 1943 (RNK!).

B. scandicum. Near Tol Abisko, 14 specimens were found in an apparently primary biotope (Palm!). June 26, 1947: on the lower course of Nissonjokk (*Regio betulina*) on a small, barren island of rock and alluvial sand; succeeding

species: *Bledius poppiusi* Bernh. and *arcticus* J. Sahlb., and a few other species of *Bembidion* (including 1 specimen of *B. siebkei*).

B. schüppeli. According to HOR (*in litt.*) the species should not be called "boreo-montane."—Transbaikal (ROU, *Folia Ent.,* 2, Prague, 1938).

B. semipunctatum. Skå Lomma, clay pit near the sea, September 16, 1947, 1 specimen (NYH); Sandhammaren, Tyke-å, June 28, 1947, 1 specimen (WSJ!). Gtl Östergarn. Sandviken, seashore, June 6, 1948, 1 specimen (WSJ!)*.

B. siebkei. Near Tol Abisko, September 10, 1947, several specimens, on a sandbank in Nissonjokk where *B. scandicum* was found by Palm (SJB!); also several immature specimens—Tol Abisko, spontaneously flying, June 26, 1948 (Palm).

B. stephensi. Sa Joutseno (THG).

B. tinctum. Thanks largely to the revision of the entire Finnish material of *B. "dentellum,"* the area has been considerably enlarged (Fig. 118).—Mdp Attmar, Lucksta, May 15, 1945, 1 specimen (HLD!). Tol Silkimuotka, June 23, 1947, 2 specimens, Måljotjokk, June 24, 1948, 1 specimen, (*Regio betulina*) (HLD!).—Nl Esbo (SBF, MH!). St Nordmark (WKS, MH!). Kb Nurmes (SBJ, MH!). Om Vetil (NSL, Åbo Academy!). Ob Oulainen (SDM, MH, according to HLL); Pudasjjärvi (SBJ, ENW, MH!); Kemi (ENW, MH!) Ok Ruhtinassalmi (SSK, 3 specimens, MÅ!). Li Ivalo, July 22, 1937 (RNK, coll. KNG!).

B. transparens. There is no reason to doubt the locality 34 Melbo.—Oa Lappfjärd, 1944 (LBH). Sb Jorois (leg ?, coll. STK!).

B. unicolor. According to HLL (N. E., 26, 1946, p. 76) the species should again be called *B. mannerheimi* C.R. Sahlb.

B. ustulatum. Ösel, (ŠZL, 1942, p. 183).

B. varium. Hll Halmstad, 1 specimen (FGQ, RM!). Ble Jämjö, Färsksjön, July 28, 1945 (SDH!). Gtl Sandön, seashore, July 7, 1946, 1 specimen (JNS!). —The locality Nl Åggelby (KNG) has to be excluded (= *B. obliquum*!).

B. velox. Lyl Tärnafors (440 msl) and Umasjö (520 msl, up to *Regio betulina*), 1945, numerous specimens (FRD!).—Kc Ontrosenvaara (Laamanen!).

B. virens. Hls Granön, July 17, 1947, 1 specimen (HLD!). Lyl, several localities in the Tärna region (up to 715 m, lowest *Regio betulina*), sometimes numerous, 1945–1948 (FRD!). Nbt Kihlangi, June 1947 (Palm). Tol Nedre-Soppero region, 3 localities, June 1948, several specimens (HLD!).—Ks Salla, Kusta, June 23, 1937, 2 specimens (KNG!).

Blethisa multipunctata. Lyl Vapstdalen, Gränssjön, *Regio betulina* (570 msl), June 30, 1946, 1 specimen (FRD). Tol Silkimuotka, Måljotjokk, *Regio betulina*, June 25, 1948, 1 specimen (HLD!).

856 Spontaneous flight, Upl Ängby, May 26, 1946, during bright sunshine (LTH); upon exposure to sun in glass, Ab Lojo, July 1945 (KRH).

*This record was not included while discussing the fauna of the islands.

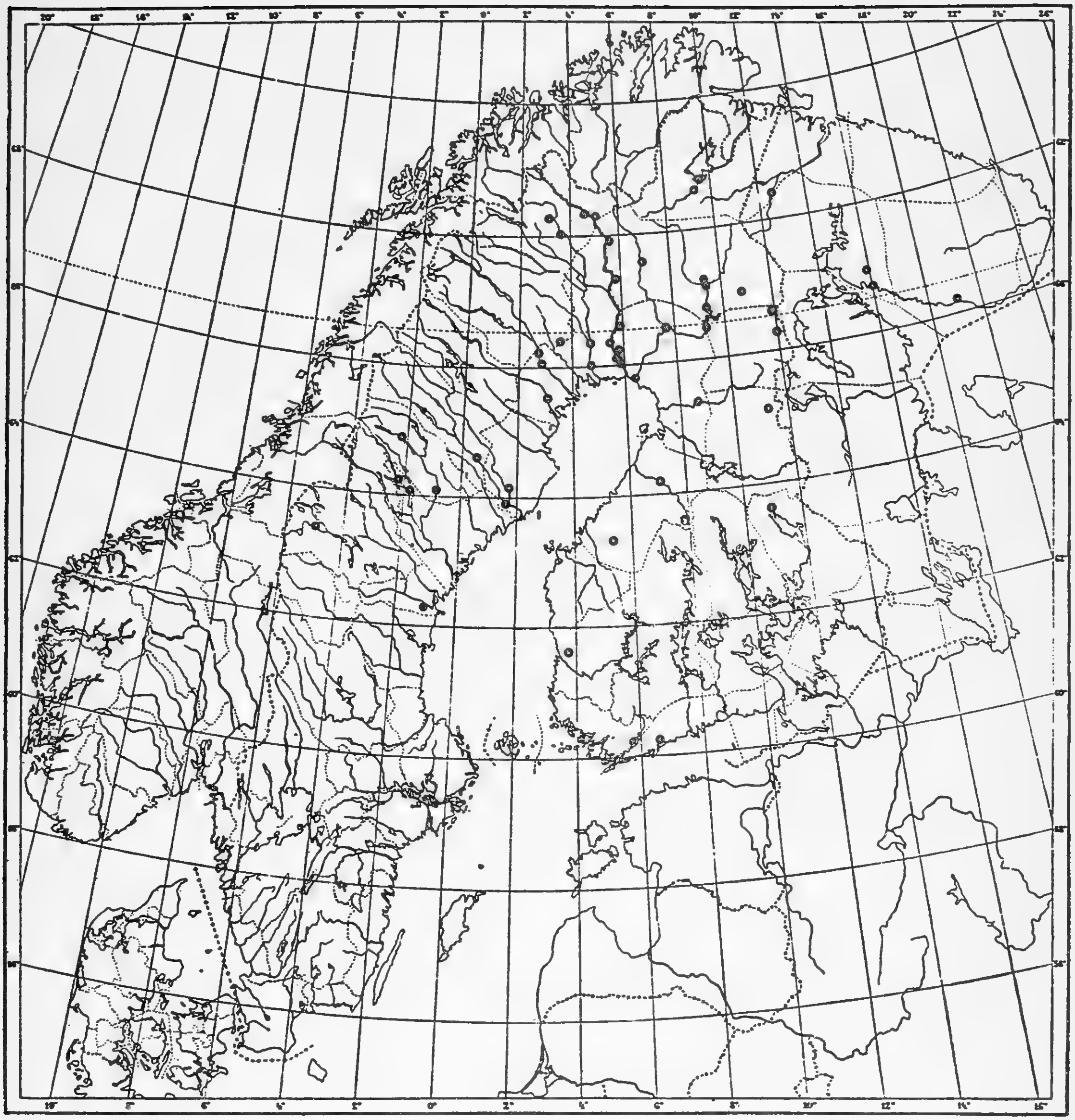

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Fig. 118. *Bembidion tinctum* Zett.

Brachynus crepitans. Ögl Mogata, numerous specimens in company with *Agonum dorsale*, August 1946 (LTH). Sdm Mörkö (Ekström, 1828, p. 50).—Nl Hangö, Tulludden, 1 specimen, strayed to the seashore, August 27, 1945 (PME, S. H. A., 11, 1945, p. 185).

According to HOR (*in litt.*) the species often occurs in Germany without *Agonum dorsale*.—Spontaneous copulation, June 9, twice (Gtl), June 10, June 19 (Öld), in captivity again on June 21, June 25. 1 specimen, not fully sclerotized, August 8, 1946 (Ögl Mogata).—In captivity fed exclusively with bread up to 18 months; also feeds on dead conspecific specimens and all kinds of crushed insects.

Bradycellus collaris. Kc Solovetsk, Anserek (LEV, MH!).

Near Hjd Tänndalen, 1 specimen in *Regio alpina* (July 16, 1944, FRD!).—likes to feed on crushed conspecific specimens in captivity.

B. harpalinus. Ik Koivisto, July 1935, 2 specimens (Paulomo, N. E., 28, 1948, p. 62; MH!). Moreover in MH there is 1 specimen, Ok Ruhtinassalmi (SSK!), which may be wrongly labeled.

In the section on "Ecology," there is a lapsus calami: "bog regions" ("Moorgebiete")† instead of moss regions (Moosgebiete")†.

B. similis. Ble Torhamn, August 7, 1946 (SDH!).

1 specimen caught in flight trap by OSS (Vgl Skara, September 1947!).

B. verbasci. Numerous specimens on flowers, especially thistles (West, 1947, p. 14).

Broscus cephalotes. Notwithstanding the observations above (p. 574) this species is capable of flight at least in some parts of its area or at certain times. There is evidence of flight from Holland (*Tijdschr. v. Ent.*, 70, 1927, p. XII; *Ent. Berichten*, 12, 1948, p. 312).

Calathus ambiguus. Sdm Mörkö (Ekström, 1828, p. 50).—Al Kökar, August 7, 1941, 1 specimen (LBÅ!). Om Nedervetil, September 17, 1943, 1 specimen (LBÅ!); if there is not a mix-up of labels here this may be a case of accidental anthropochorous transport.—Sv Pisi, August 19, 1942, 1 specimen (PME, 1946, p. 38).

Numerous immature beetles, June 11–14, 1947 (Öld Greby Alvar)††.

C. erratus. 20 Sundalsören (coll. KLF!). 36 Målselv, Solvang, June 20, 1930, 1 specimen (JEN!).

In captivity likes to feed not only on bread but also on crushed conspecific specimens, other species of *Calathus* and flies.—In Sv immature beetles as late as July 20, August 14 (PME, 1946, p. 38).

C. fuscipes. Sv Kuuttilahti, June 19, 1942, 3 specimens (PME, 1946, p. 38).

Fossil record: Ireland, late-glacial (Jessen and Farrington, 1938, p. 241).

†(suppl. translator).

††(Plant community consisting typically of mosses and calciphilous harbaceous plants that grow on steppelike shallow alkaline soils overlying Scandinavian limestones; suppl. scient. edit.).

C. melanocephalus. Kl Valamo (Y. Kangas).

In Sv immature beetles as late as September 14, September 22, September 28 (PME, 1946, p. 38).

C. micropterus. In Sv several immature beetles from mid-August through September (PME, 1946, p. 38).

C. mollis. In northern Europe the species is divisible into two well-defined subspecies, which are also geographically separated:

Forma typica is the western form, which is generally somewhat larger with more slender body and longer legs. The dorsal side is almost uniformly pitch brown or yellowish-brown (only on Bornholm almost constantly paler brownish-yellow), always without sharp contrast in color between pronotum and elytra. The right paramere always with a distinct tooth (LTH, E. T.,
857 1943, p. 53, Fig. 25C). To date I have seen only macropterous specimens. Record specimens were studied from Norway (numerous specimens), Jutland (in large quantities), Bornholm (Slusegaard, numerous specimens), and England (5 specimens).

Subspecies *erythroderus* Gaut. is the eastern form, which in Sweden occurs exclusively. It is stouter, with shorter legs; there is a definite color contrast between the pale pronotum and the more or less darkened elytra and head. The females are more dull. The right paramere of the male has at the most the hint of a dorsal tooth, but mostly it is quite unarmed (LTH, l.c.; Fig. 25a, b). This form shows wing dimorphism (Fig. 25, p. 340). Outside Sweden only record specimens from Bornholm and Sjaelland were seen (Jaegerspris, Kulhus, 1862, ♀, Copenhagen Museum!).

Within the region both forms occur only on Bornholm. According to the records from Mecklenburg (GRD, 1937, pp. 81–82) the structure of the parameters goes for that region too.

Several immature beetles, June 11–16, 1946 (Öld Greby).—Fed with bread in captivity and also with a crushed *C. erratus* (Öld).

Calosoma inquisitor. Distribution map also given by HNR, 1933, p. 313.—Små Visingsö, June 1947, numerous specimens (HEQ).

C. sycophanta. Skå Barkåkra, Vejby-strand, 1 dead specimen on the seashore, July 8, 1946 (WSL). Vgl Horred, July 1941, one flying specimen (L. v. Post, jr., coll. LTH).—Jutland Rye, 1942 (West, 1947, p. 9).—According to Benick (1947), in northwestern Germany too *C. sycophanta* is a transmigrating (not native) species.

Carabus arvensis. Upl Älvkarleö, May 1946 (Rapp). Gst Gävle, 1946 (Rapp). —Ösel (SZL, 1942, p. 182).

C. auratus. In captivity the larva is partly cannibalistic (LNG, 1921, p. 76). The beetle also feeds on fungi (l.c., p. 47) and fruit, in captivity it likes to feed on bread (Jung, 1940).

C. cancellatus. Ko Petrosavodsk, 1944, 1 specimen (PHJ).

Immature beetle, August 22, 1948 (Hll Harplinge).—In captivity the beetle

likes to feed on bread (Jung, 1940).—Near Ta Juupa River in 1945 KNG found numerous specimens, but had never found the species from 1922 through 1931 despite intensive collecting. He holds that a new immigration has taken place (*in litt.*).

C. clathratus. Ösel (SZL, 1942, p. 182).

C. coriaceus. Dlr Enviken, Övertänger, May 14, 1941 (K. Danielsson, according to KLF); Lima, Tandberget (600 msl), dry coniferous forest soil with tall *Calluna* July 3, 1941, 1 specimen (OLS!). Hls Marmaverken, 1944, 1 specimen (HLD!).

The beetle likes to feed on bread in captivity (Jung, 1940).

C. glabratus. Kn Maaselkä (Peltonen!).

C. granulatus. Vrm Östmark, Rännberg, July 27, 1935 (R. Broberg). Dlr Enviken, Marnäs, 1945 (Ruth Skogblad, according to KLF). Hls Bergvik, April 5, 1945, 2 specimens (HLD!).

Copulation, June 10, 1947 (Skå Hälsingborg, PLQ).—The beetle likes to feed on bread in captivity (Jung, 1940).

C. hortensis. Distribution map also in HNR, 1933, p. 317.

C. menetriesi. Especially "in very boggy, sparse pine forests with a thick layer of moss"; Sv (PME, 1946, p. 18).—Imago, May through mid-June and mid-August through September (Sv; PME, l.c.).

858 *C. nemoralis*. Vrm Östmark, Rännberg, since 1935, more frequent in recent years (R. Broberg). Hls Bergvik, 1945, frequent (HLD!).—Sv Pisi (PME, 1946, p. 19); Mjatusova, Lodeinoje-Pole, 1944, 1 specimen (PHJ).

Spontaneous copulation, April 17 (Upl), May 27 (Denmark; West, 1947, p. 9), June 10 (Skå, PLQ).—Seen fighting with a small (uninjured) *Lumbricus* (Upl Djursholm, May 1947). The beetle likes to feed on bread in captivity (Jung, 1940).

C. nitens. Hjd Lillhärjeån, 1947, 1 specimen (HLD). Jtl Anjan, Steuker, *Regio alpina* (650 msl), *Calluna-Empetrum* heath, June 19, 1945, 1 specimen (H. Kauri).

"A species of sunny fine-sandy ground, and accordingly a characteristic animal of the flood-bank of Lake Ladoga"; Sv (PME, 1946, p. 19).—In eastern Karelia also found in late summer and autumn (September, October) (PME, 1946, p. 19); Nl Tvärminne, August 11, 1947 (PME!).

C. violaceus. Sb Vehmersalmi, July 1942, 1 specimen (HDL).

Chlaenius nigricornis. Kontiolahti (Finland): Tb instead of Kb.

According to PME (1946, p. 29), the species in Sv may have the same change of habitat as in *C. tristis*, etc.—Immature beetle, August 3, 1946 (Ögl Mogata).

C. quadrisulcatus. Undoubtedly this species at: Små Balaryd, Skärsjö (Ljungh, 1823, p. 271, "*Harpalus sulcicollis*").—Sv Obzha, fragment (PME; 1946, p. 29).

C. tristis. Ble Torskors, July 1947, numerous specimens (NYH!). Öld Halltorp, *Carex-Amblystegium* swamp, June 11, 1946, 1 specimen (LTH).

Found under moss, at least 2.5 km distant from water, in its winter habitat (NBG, *in litt.*).—A full-grown larva (Upl Djursholm, August 1942) in captivity fed on freshly killed *Lumbricus, Charaeas, Serica*, tachinids.

C. vestitus. Jutland Hadsten (West, 1947, p. 12).

The hypothesis of adult hibernation is being confirmed by a find of 4 immature beetles on September 8, 1946 (Skå Lomma, NYH).

Cicindela campestris. Skå St Olof, June 28, 1943 (FRL).

Still frequent on June 19–21, 1947 on Öld Greby Alvar†, spontaneous copulation observed on June 19 and 21.

C. silvatica. Sdm Mörkö (Ekström, 1828, p. 50). Nbt Pajala; Kihlangi, Muodoslompolo; June 1947, numerous specimens (Palm). Tol Abisko, dead specimens, along railroad tract, August 1944 (LDN!).

In Sv already found on April 29 (PME, 1946, p. 17).—1 specimen was observed catching and eating an individual of *Formica fusca* (Vbt Kulbäcksliden, June 18, 1939, FRL). The larva even attacks large butterflies (*Satyrus*) and Odonata (Öld; ADZ, E. T., 1912, p. 159).

Clivina collaris. In Böhemia always on more or less sandy soil (Kult, *in litt.*).—Attracted to light, June 1942 (Böhemia, Kult).

C. fossor. Tol Silkimuotka, June 23, 1947 (HLD!).—Ösel (SZL, 1942, p. 182).

Spontaneous flight, Lyl Tärna, July 3, 1945 (FRD).

Cychrus caraboides. Hls Bergvik region, 3 localities (HLD). Lul Virihaure, *Regio betulina*, July, August 1945, 2 specimens (BRK).

Immature beetle, July 9 (Sv; PME, 1946, p. 18).

Cymindis angularis. Sdm Mörkö (Ekström, 1828, p. 50).—Sa Joutseno, 1936 through 1944, 3 specimens (THG! BLQ).—Sv Gumbaritsa, July 14, 1942, 1 specimen (PME, 1946, p. 42).

Copulation in captivity, June 25, 1947 (Öld).—The beetle likes to feed on bread.

C. humeralis. Immature beetle, June 13, 1947 (Öld Halltorp).—In captivity likes to feed on bread.

859 *C. macularis*. Al Eckerö, Torp, 1943 (LBÅ).

In captivity feeding on bread as well as on a crushed *Calathus* (Öld).

C. vaporariorum. Upl Älvkarleby, September 4, 1945 (ELS!).—Ösel (SZL, 1942, p. 186).

Demetrias imperialis. Gtl Fårön, Ava, on the seashore (permanently?), June 16–17, 1946, 6 specimens (Palm, E. T., 1947, p. 171!). Sudersand, June 20, 1947, 1 specimen (Åberg!). Sdm Öster Malma, June 1946, 2 specimens

†(Plant community consisting typically of mosses and calciphilous herbaceous plants that grow on steppelike shallow alkaline soils overlying Scandinavian limestones; suppl. scient. edit.).

(HLD!).—Denmark, south coast of Lolland, 1946, 1 specimen, together with *D. monostigma* (West, 1947, p. 17).

D. monostigma. Öld Högsrum, Gladvattnet, June 20, 1947, numerous specimens (LTH). At the locality Vrm Visnum-Kil several specimens in spring of 1946 and 1947 (WRN).

Diachila arctica. Tol Karesuando, Maljotjokk, June 24, 1948, 1 specimen, in the stomach of a trout (HLD!).

In Norway there seem to be no records from the *Regio alpina* (STA, 1946, p. 73).

Dichirotrichus pubescens. Doubtful: Sdm Mörkö (Ekström, 1828, p. 50. "*Harpalus pubescens*": ? = *Trichocellus placidus*!).

In Schleswig-Holstein the beetle attacked the heart shoots of young *Beta* plants (HOR, *in litt.*).

D. rufithorax. Ögl Linköping, September 1947, 1 specimen (OSS!). Vrm Varpnäs, September 1947, 1 specimen (OSS!); Kristinehamn, among weeds in a garden, 1945, 1946, several specimens (WRN).

Both specimens were collected by OSS in his flight trap.

Dolichus halensis. Skå Ven, 1942, 1 specimen (P. Prytz, according to LDN).

Numerous specimens flying to artificial light near Temesvár in Hungary (Dorn, 1946).

Dromius agilis. Tol Abisko, drift material on the seashore, June 1947 (Palm).—Ko Petrosavodsk, June 11, 1944 (Kontuniemi! KRV).

Flying to light, June 28, 1944 (Ble Rödeby, SDH!).

D. angustus. Skå Hälsingborg, Raus-marker, under bark at the foot of an old *Pinus*, April 14, 1947, February 1, 1948, numerous specimens (PLQ!). Boh Lycke, under bark of *Pinus*, February 2, February 17, March 1, 1949, 3 specimens (O. Pehrsson!). Gtl Stenkyrka, July 1944, 1 specimen (OTT!); rediscovered in Sandön, June 1947, 2 specimens (WRN).

D. fenestratus. Dlr Orsa, 1947 (SJB). Jtl Bispfors, 1946 (Palm).—Oa Lappfjärd, 1944 (LBH); Vasa (Kontuniemi!).

D. linearis. Små Vissefjärda, June 13, 1944 (LBÅ). Gtl Fårön, July 11, 1947, 2 specimens (KMK!).—Al Eckerö, Skog, 1943 (LBÅ).—Sv Kuujärvi, August 10, 1942, 1 specimen (KAN!).

In West Germany not xerophilous, but found mostly at moist places (HOR, *in litt.*).—Immature beetles, June 9 (Gtl), September 21 (Skå). Spontaneous copulation, June 17 (Gtl), August 22 (Hll).

D. marginellus. Hls Bergvik, 1944–1945, several specimens (HLD!). Jtl Bispfors, 1946 (Palm).—Al Eckerö, Torp, 1943 (LBÅ).—Sv Gumbaritsa (PME, 1946, p. 41).

Spontaneous flight, Nl Tvärminne, July 25, 1948 (PME).

D. nigriventris. Dlr Hagge, May 20, 1944, 1 specimen (OTT!). Hls Bergvik, April 19, April 22, 1947, 2 specimens; Tönnebro, April 16, 1947, 1 specimen (HLD!).—6 Kvitsöy, July 1930 (MID, coll. JEN!).

Spontaneous copulation, June 12, 1946 (Öld Greby).

D. quadraticollis. Sv Ulvana, June 5, 1944, 1 specimen (KAN!).

D. quadrimaculatus. Vrm Visnum, September 1944, (JNS); Östmark, Rännberg, June 19, 1936 (R. Broberg). Upl Älvkarleby, May 1945, 1 specimen (ELS!).—Ab Korpo, 1945 (WEG).—Ösel (SZL, 1942, p. 186).

860 Also near Göteborg repeatedly found under bark of *Pinus* (SDN, LTH).—Flying to light, July 25, 1947, 10:00 p.m. (Upl Djursholm). Collected in flight trap by OSS (Ögl, Upl).

D. quadrinotatus. Hls Bergvik, November 20, 1945, 2 specimens (HLD!).—Several new localities in Jutland, 2 in Fyen (West, 1947, p. 18).

In the top of a pine, August 17, 1945 (Upl Stocksund, FRL!).—Immature beetle, August 21, 1945 (Ble Sjöarp, HEQ!).

D. sigma. Boh Sämstad, August 2, 1946, 2 specimens (HLD!).

Dyschirius aeneus. Gtl Fårön, Ava, sea drift, June 16, 1946, 1 specimen (Palm!); Sandön, June 23, 1947, 1 specimen (WRN!).—Nl Helsinge, July 9, 1941, 1 specimen, together with *D. lüdersi* (STK, coll. PME!). Kl Parikkala, 1945, 1 specimen (HLL!).—Sv Ulvana, July 25, 1943, 1 specimen (KNG!).—Latvia, 2 localities (LCK, 1942, p. 173).

Flying upon exposure to sun in glass (Bohemia, Kult, *in litt.*).

D. angustatus. Kn Karhumäki, Kumsa River, July 28, 1942, 1 specimen (PRT!).

D. helléni. Lyl Tärnaby, *Betula nana* moors, June 1, 3 specimens, July 11, 2 specimens, 1946; Strimasund, Kåtaviken, moor, 525 msl, July 18, 1946, 1 specimen, Abelvattnet and Virisen, July 13 to August 2, 1947, 4 localities, 8 specimens, all in *Betula nana* moors; only in *Regio betulina* (FRD!). Tol Karesuando, *Sphagnum fuscum* moors, June 1947 (Palm).—Lk Pallastunturi, July 12, 1938, 1 specimen (KNG!). Le Ounastunturi, July 22, 1932, 1 specimen (RNK, coll. HDL!).

D. impunctipennis. In 1931 rediscovered by JNS in Gtl Sandön (E. T., 1935, p. 62).

D. lüdersi. Latvia (LCK, 1942, p. 173).

D. nitidus. Sv Segezha, May 25, 1943, 2 specimens (PME, 1946, p. 22).—Latvia Libau, 1938 (LCK, 1942, p. 171).

Spontaneous flight observed in Bohemia, May 1942 (Kult, *in litt.*).

D. obscurus. Ko Soutjärvi, June 9, 1943, 10 specimens (KNG!).

Flying in large numbers during hot sunshine. May (Germany, Memmert; Alfken, 1924, p. 386). Food, see p. 545.

D. politus. Gtl Fårön, Ava, sea drift, June 16 to 17, 1946 (Palm).

Spontaneous flight near Prague (Kult, *in litt.*).

D. "*rufipes*". Comparison with *D. rufipes* identified by G. Müller showed that the specimens from Ik and Kl belong to a different species, which is closest to *D. importunus* Schaum or is to be considered as its subspecies. A definite conclusion is awaited.

The Fennoscandian specimens have fully developed wings.

D. septentrionum. Nbt Kihlangi, June 1947 (Palm). Tol Nedre-Soppero, July 1, 1948, 1 specimen (HLD!); Karesuando, June 1947 (Palm).

D. thoracicus. Hls Tönnebro, 1947 (HLD!); Storjungfrun, 1945 (HLD!); Hudiksvall, Maln, 1943 (WSJ!).

Food, see p. 545. According to SDT (1867, p. 503) the larva feeds on adults and larvae of *Bledius* as well as *Heterocerus.*—1 specimen caught flying upon exposure to artificial light (Öld Hornsjön, June 15, 1947).

Elaphrus angusticollis. Sv, bank of the River Segezha, 2 specimens (PME, 1946, p. 21).

The size of the wings varies but attains hardly more than 60% of the surface area of the wing of *E. riparius.* At least in Fennoscandia the species is to be considered flightless.

E. cupreus. Lyl Tärna region, 5 localities, 1945 to 1946 (FRD!), among them 2 specimens (Nuolpträsk) in the lower *Regio alpina* (825–835 msl).

Numerous young larvae, July 12 (Denmark; West, 1947, p. 10).

861 *E. lapponicus.* Lyl Tärna, Laxfjäll, *Regio betulina* (730 msl)[†], June 25, 1945, 1 specimen (FRD!). Lul Virihaure, Staloluokta, *Regio betulina* (600 msl), July 15, 1945, 1 specimen (BRK).

1 specimen in winter abode in a *Sphagnum* hummock (Tol Abisko, September 1947, SJB).

E. riparius. Spontaneous flight, May 29, 1946, 6:30 p.m. (Skå Hälsingborg, PLQ).

E. uliginosus. Ögl Mogata, on the seashore, August 1946, 1 specimen (LTH).

Harpalus aeneus. Spontaneous copulation, August 5, 1946 (Ögl Söderköping). Likes to feed on bread and crushed conspecific specimens (Öld Greby).

H. anxius. Hll Halmstad, etc., May 1944, several specimens (FGQ, RM!).

Copulation in captivity, June 21, 1946 (Öld Stora-Rör). Likes to feed on bread as well as crushed conspecific specimens (Öld). In captivity numerous flying males and females at artificial light (Öld).

H. azureus. Spontaneous copulation, June 10, 1946 (Öld Greby); later, in captivity, again on June 22 and 23. Immature beetles: Gtl Fardume, August 10, 1923; Visby, August 26, 1928.—In captivity likes to feed on bread (Öld).—Six specimens flying to artificial light near Temesvár in Hungary (Dorn, 1946).

H. calceatus. Skå Löderup, August 1948, numerous specimens (LDN); Vitemölla, July 22, 1947, 1 specimen (TJB); Ivö, August 20, 1946 (SDH). Hll Harplinge, Särdal, August 19–21, 1948, 2 living specimens, 1 dead specimen, on sandy soil, close to the sea (LTH). Boh Lycke, August 20, 1946, 1 specimen (Olof Pehrsson!). Gtl Fårön (MJB, 1 specimen VA!); Sandön, June 1947, 1 specimen (WRN). Upl Värmdön, Väster-Skägga, 1945, 1 dead specimen (LTH).—Nl Kottby, 1945, 1 specimen (HLQ, coll. KNG). Ta

[†](cf. p. 846; suppl. scient. edit.).

Ruovesi, Siikakangas, August 15, 1943, 1 specimen (PME!).

Numerous specimens flying to light near Skå Löderup, August 1948 (LDN, 1948). 1 specimen near Nl Kottby (HLQ).

H. distinguendus. Im Muolaa, 1 specimen (PME!).—Ösel (SZL, 1942, p. 184).—According to SZM not known in North Africa (but known in Madeira and Azores) (*Atti Soc. Ital. Sci. Nat.,* 80, 1941, p. 58).

Immature beetle, July 29, 1945 (Upl Värmdön).—In captivity feeding on bread as well as pieces of *Lumbricus* and a crushed elaterid larva (Upl Djursholm).

H. frölichi. Skå Södra-Sandby, Skatteberga, August 20, 1944 (CHR); Fågelsång, April 4, 1924 (Kullander, coll. LDN!). Öld Vickleby, Stora-Frö, August 1943, 1 specimen (KMN; NYH, O. E., 1945, p. 154; ML!); Resmo Alvar,[†] September 16, 1946, 1 specimen (ML, according to NYH).

Flew to artificial light, as well near Warsaw (MAK, *in litt.*) as in Böhemia (*Acta Soc. Ent. Böh.*, 1910, p. 16, according to Kult, *in litt.*).

H. fuliginosus. Dlr Malingsbo, 1941, 1 specimen (FRL!); Norrbärke, Björsjö, May 29, 1947, 1 specimen (OTT!).—Latvia Libau, 1936, 1 specimen (LCK, 1924, p. 175).

H. griseus. Skå Vitemölla, July 20, 1947, 1 specimen (TJB!); Löderup, August 1948, frequent (LDN). Ble Bräkne-Hoby, Sjöarp, August 6, 1939, 1 specimen (KNG!). August 30, 1945, 1 specimen (HEQ!). Hll Östera-Karup, August 7, 1944, 1 specimen (SJB!); Harplinge, Särdal, August 18, 1948, 1 specimen (LTH). Vgl Skövde, August 23, 1944, 1 specimen (FRD!). Öld Kastlösa, Väderstad, August 16, 1946, 1 specimen (HZE!). Gtl Fårön, Norsta-aura, June 21, 1947, 1 specimen (Åberg!); Sandön, July 7, July 8, 1946, 2 specimens (JNS!).—Ik Muolaa, June 28, 1938 (MER, coll. HDL!). Jutland, Mols (West, 1947, p. 13).

Copulation in captivity, August 2, 1948 (Skå Löderup, LDN).—Mass flight to light, August 1948 (Skå Löderup, LDN, 1948).

H. hirtipes. Skå Hässleholm July 17, 1947, 1 specimen (PLQ). Öld Ottenby, July 23, 1941 (LDN!).

In captivity feeding on bread as well as on a crushed fly (Öld Stora-Rör). Spontaneous flight to artificial light, observed in Bohemia (*Acta Soc. Ent. Böh.,* 1910, p. 16; according to Kult, *in litt.*).

862 *H. latus*. Immature beetle, April 12 (Sv; PME, 1946, p. 31).—Spontaneous flight in the evening. Sb Vehmersalmi, July 1946 (HDL).

H. luteicornis. Hll Halmstad, Eketånga, July 26, 1943, 1 specimen (LDN!). Gtl Fårösund, June 30, 1946, 1 specimen (JNS!); Fårön, 1901, 1 specimen (Lindbom!), Broa, June 15, 1946, 3 specimens, Ava (sea drift), June 16, 1946, 1 specimen (Palm!).—Ab Korpo, June 13, 1944, 1 specimen (WEG!). Ta Hattula, May 27, 1940, 1 specimen (WEG!).

[†](cf. p. 866; suppl. scient. edit.)

In Sv on sandy soil with sparse vegetation, partly found in open terrain and partly in sparse mixed forest (PME, 1946, p. 31).

H. melancholichus. Jutland Mols (West, 1947, p. 13).

1 specimen flying to light (Skå Löderup, August 2, 1948, LDN, 1948)*.

H. melleti. Gtl Fårön, Broa, June 15, 1946, 2 specimens (Palm).

Near Gtl Visby partly in the company with *H. rupicola* and *H. punctatulus* at the locality described for the former and partly in a downtown ruin on much more shady, somewhat moister, humus-rich soil.—In captivity fed with bread (GTL).—Numerous specimens observed spontaneously flying to artificial light (Böhemia; Kult, *in litt.*).

H. neglectus. Hll Söndrum and Övraby, 1 specimen each (FGQ, RM!). Gtl Eksta, Djupvik, May 31, 1948, 6 macropterous specimens (WSJ!)*. Several new Danish localities (West, 1947, p. 13).

In captivity feeding on bread as well as on crushed flies (Öld).

H. picipennis. Skå Vitemölla, July 29, 1947, 1 specimen (TJB!).

In Bohemia 1 specimen observed during spontaneous flight, May 17, 1936 (Kult, *in litt.*).

H. pubescens. Immature beetles, May 14 and August 12–20 (Sv; PME, 1946, p. 30).—Mass flight to light in Hungary (Dorn, 1946).

H. punctatulus. Gtl Sandön, June 1947, 2 specimens (WRN).—Near Ka Viborg, probably in 1928. Ab Korpo, 1945 (WEG). Sa Villmanstrand, August 21, 1945, 2 specimens (THG!); Joutseno, August 23, 1945 (BLQ).—Ösel, 1934, repeatedly found (LCK, 1942, p. 175; SZL, 1942, p. 183). Latvia, 2 localities (LCK, l.c.).

Numerous specimens (more than 100), April 28, 1945, June 18, 1946, at the locality near Gtl Visby described under *H. rupicola* (strangely, not observed here earlier).—Numerous specimens in umbels of *Daucus* (Denmark; West, 1947, p. 12). In captivity fed as well with bread (some exclusively) as with crushed carabids and flies (Gtl).—After a two-day stay on wet substratum one male flew in the evening during artificial light, July 1, 1946 (Gtl).

H. puncticeps. Skå Färslöv, July 9, 1947, 1 specimen (Matthiessen!). Öld Vickleby, 1944, 1 specimen (LBA!), 1946, 1 specimen (WRN!); Halltorp, 1946, 12 specimens, 1947, 2 specimens (LTH); Greby, 1946, 1 specimen (LTH). Ik Muolaa, May 28, 1938, 1 specimen (PME!).—Several localities in Jutland and in Fyen (West, 1947, p. 13, and *in litt.*). Calabria (SZM, *Atti Soc. Ital. Sci. Nat.*, 80, 1941, p. 57).

In captivity fed with bread (Öld).

H. puncticollis. Sdm Vagnhärad, Stensund, April 10, 1944, 1 specimen (Matthiessen!). Ösel (SZL, 1942, p. 183).

H. quadripunctatus. Hjd Tänndalen, July 18, 1944 (FRD).

*This record could not be taken into consideration above.

In northern Norway right into highest part of the *Regio betulina* (STA, 1946, p. 96).

H. rubripes. Vrm Väse, 1945, 1 specimen (WRN).

In captivity feeding as well on bread as on crushed conspecific specimens
863 (Öld). One male flying in captivity (Öld). Spontaneous flight of a male during
hot sunshine, June 21, 1947, 10:30 a.m. (Öld Greby).

H. rufitarsis. Öld Vickleby, June 15, 1946, 1 specimen (WRN!).—Calabria (SZM, *Atti Soc. Ital. Sci. Nat.*, 80, 1941, p. 58).

In captivity fed with bread (Öld). One female flying during artificial light (Öld).

H. rupicola. In captivity fed with bread (Gtl).—One male flying during artificial light (Gtl).

H. seladon. Dlr Söderbärke, Gläfse, June 20, 1947, 1 specimen, Larsbo, July 5, 1947, 2 specimens (OTT!).—Ka Hogland, July 2, 1939, 1 specimen (THG!).—Sv Pisi, June 14, 1942, 1 specimen (PME, 1946, p. 30).—Ösel (SZL, 1942, p. 183, *H. "brevicollis"*).

In captivity fed exclusively with bread (Öld, Upl). Flying to light near Warsaw, 1947 (MAK).

H. serripes. Spontaneous copulation, June 10, 1946 (Öld Greby), in captivity on May 4, 1945 (Gtl). Immature beetle, July 27, 1946 (Öld Borgholm, SDH!). One specimen lived in captivity from April 1945 through January 1948.—The beetle can be fed exclusively with bread; fed on a crushed *Tenebrio* too. Spontaneous flight near Prague, May 16, 1946 (Kult, *in litt.*).

H. servus. Hll Harplinge, Särdal, in loose sand under *Calluna*, August 19, 1948, 6 specimens (LTH).—Öld Stora-Rör, in loose sand under *Calluna*, June 12, 1947, 3 specimens (LBL, LTH).

H. smaragdinus. Ble Torhamn, August 7, 1946, 4 specimens (SDH!). Gtl Fåron, July 10, 1947 (KMK!). Vrm Väse, 1945, 1 specimen (WRN); Torsby, Sörbo, August 10, 1944, 1 specimen (SVS!).

Copulation in captivity, July 28, 1946 (Öld). Likes to feed on bread and crushed *Harpalus* (Öld).—Spontaneous flight of one individual to artificial light (Skå Löderup, August 2, 1948, LDN, 1948).

H. tardus. Kc Tiiksa, June 1943, 1 specimen (Laamanen!).

In captivity feeds on bread and crushed conspecific specimens (Gtl).

H. vernalis. Gtl Visby, on the eastern city wall, April 30, 1945, 1 specimen (LTH).

In captivity fed with bread (Öld).

H. winkleri. Ta Lammi, June 18, 1946, 2 specimens (J. Kangas!). Ik Muolaa, 1938, 1 specimen (MER, coll. HDL!).—Kn Karhumäki (CRP, coll. STK!). Latvia (LCK, 1942, p. 175).

Lebia chlorocephala. Vrm Östmark, Rännberg, 1935, 1936 (R. Broberg). Dlr Enviken, Övertänger, 1945 (Karin Eriksson, according to KLF). Hls Bergvik, 1945. Långvind, 1947 (HLD!); Färila (LBL).

Copulation in captivity, August 19 (Ögl). Immature beetle, August 6, 1946 (Ögl Mogata).—Numerous specimens on *Hypericum* in company with *Chrysomela varians* larvae in June (Denmark; West, 1947, p. 17). In captivity the beetle also feeds on bread.—Spontaneous flight in the evening in July 1946, Sb Vehmersalmi (HDL).

L. crux-minor. Vrm Östmark, Rännberg, 1945, (R. Broberg).

Repeatedly flying in glass upon exposure to sun, May 27, May 31, 1946 (Upl).

L. cyanocephala. Ögl Mogata, August 11, 1946, 1 specimen (LTH); St Anna, April 7, 1947, 1 specimen (WSJ!).—Ösel, (SZL, 1942, p. 186).

In captivity, 1 specimen flying during high room temperature, June 26, 1946 (Öld Stora-Rör).

864 *Leistus ferrugineus*. Lyl Tärna, Rövattsliden, *Regio betulina* (685 msl). July 1, 1945, 1 specimen *Regio coniferina*, May 25, 1946, 1 specimen, Vapstdalen, Gräns Lake, *Regio betulina* (570 msl), June 7, 1946, 2 specimens, Abelvattensdal, several localities, all in *Regio betulina*, 1947 to 1948 (FRD!).

L. rufescens. Lyl Umgransele, July 8, 1945, 1 specimen (B. Persson!); Skalmodal (540 msl), June 26, 1947, 1 specimen (FRD).—Ko Petrosavodsk, 1943 (Hll!).—Ösel (SZL, 1942, p. 182).

Licinus depressus. Öld Greby, June 11 to 24, 1947, numerous larvae (most of them half-grown), only 2 adults (both old and damaged); one larva observed feeding on a *Vallonia costata* Müll. (det. N. Hj. Odhner) (LTH).

Lionychus quadrillum Dft.

Distribution

Sweden. The totally unexpected discovery of this species in northern Europe was made by HZE on May 27, 1945 near Nke Örebro, Oset. Subsequently (even in 1948) it was found again in large numbers (E. T., 1947, p. 120).

Absent from the rest of Fennoscandia and neighboring regions, except England, where the species occurs in the south at the south coast (Joy, 1932, p. 373).

Total area: Euro-Mediterranean species. In Europe northward as far as northeastern France (DEV, 1935–38, p. 58), Belgium and Holland (EVS, 1898, p. 101; 1922, p. 39), central Germany to Berlin region, but not east of the Oder (HOR, 1941, p. 343), eastward as far as Transylvania (PTI, 1912, p. 40) and Greece (OTZ, 1896, p. 213). Southward as far as northeastern Spain (FUE, 1921, p. 22) and southern Italy, also Sicily (LUI, 1929, p. 141).—Asia Minor (SZM, *Atti. Soc. Ital. Sci. Nat.,* 80, 1941, p. 64), Cyprus (BUR, 1939, p. 197).

Ecology

The habits of this species in Sweden have been described in detail by HZE

(E. T., 1947, p. 120). Here it lives in the dry, barren gravel of a railroad embankment constructed in 1943 in boggy terrain, especially on the southern side, strongly exposed to the sun. In the rest of Europe this species occurs at gravelly or sandy, more or less moist places mostly on riverbanks, less often if there is no connection to open water (EVS, 1898, p. 101; Arnold, E.B., 1929, p. 56). In Germany "in mountainous and hilly terrain" (HOR, 1941, p. 343). Evidently the insect is very thermophilous: it tolerates strong, continuous exposure to the sun (August 1947) with no perceptible distress.

Biology

Since copulation was observed in Italy as early as April (E. B., 1929, p. 56), it
865 may be assumed that the species hibernates as imago. Near Orebro imagines were found even in late October (E. T., 1947, p. 121), immature beetles in late August (!).

Dynamics

The wings (in the Swedish specimens) are fully developed. Hence the insect may be capable of flight, although as far as I am aware there are no observations. Repeated exposure to sunlight in a glass to induce flight (August 1947) was unsuccessful.—The species probably reached Sweden by traffic.

Metabletus truncatellus. Lyl Umgransele, 1946 (B. Persson!).

A second instar larva was found on July 7 (Upl Djursholm): molting on July 10, pupation on July 20, emergence on July 30 (LTH). It was fed on small pieces of *Lumbricus*. Three specimens observed flying spontaneously in the evening, Sb Vehmersalmi, June, July 1946 (HDL).

Microlestes maurus. Gtl Fårön, Broa, June 15, 1946 (Palm).—Ösel (LCK, 1942, p. 176; SZL, 1942, p. 186). Latvia (LCK, l.c.).

M. minutulus. Små Överum, July 1945 (JNS!).—Al Jomala, July 2, 1942 (STN, coll. WEG!); Finström, 1943 (LBÅ). Hattula is located in Ta (not "Ka").

Miscodera arctica. One specimen flying spontaneously during sunshine, May 22, 1946, 4:20 p.m. (Jtl Bispfors, Palm).

Nebria brevicollis. Gtl Sandön, June 28, 1947, 1 specimen (WRN!). Sdm Mörkö (Ekström, 1828, p. 50).

Nebria gyllenhali. In Lyl Tärna region up to 1300 msl (FRD).—2 specimens in drift material in the Torne Lake, July 1948 (Palm).—An interglacial fossil record on Iceland (Thorkelsson, 1935, p. 5).

N. livida. Kl Parikkala, 1945 (HLL).

In Sv immature beetles, June 18 and August 22, larvae during July (PME, 1946, p. 19).

N. nivalis. In drift material on the shore of Torne Lake, June 1947 (Palm).

N. salina. Boh Ljung, Direhuvud, June 24, 1945, 1 specimen (KLF). I had overlooked the record (3 specimens, Dublin County, OMH, Dublin Museum!) from Ireland (Donisthorpe, E. M. M., 65, 1929, p. 186).

Notiophilus aquaticus. In Lyl Tärna region as far as 1538 msl (FRD). Fossil records: Scotland, interglacial (Movius, 1942, p. 268). Dogger Bank, postglacial "moorlog" (Bell, 1922). (Last line: "in this" should be deleted).

N. biguttatus. The numerous new records called for a new map (Fig. 51, p. 406). In northern Finland three localities have been deleted: Lp Pitkajärvi (STÅ; 4 specimens = *N. reitteri*!); Lk Muonio (PPP; no record specimen); Kittilä, Aakenustunturi (SAA, 1917, p. 281; only one larva, which may very well belong to *N. reitteri*).—Ösel (SZL, 1942, p. 182).—In North Africa according to Koch (*Mitt. Münch. Ent. Ges.*, 1939, p. 234).

N. germinyi. Skå Ven, May 1934 (Palm, coll. LTH).—Ösel (SZL, 1942, p. 182).

Regio alpina (950 msl), Lyl Umfors, Norra-Storfjället, July 16, 1945 (FRD!).

N. palustris. The doubtful record from Jtl Åre (AND) pertains to *N. germinyi*!—Kc Ontrosenvaara (Laamanen!).

N. pusillus. Gtl Fårön, Broa, June 15, 1946 (Palm). Bornholm, 2 localities (West, 1947, p. 9). Ösel (SZL, 1942, p. 182).

866 Several immature beetles, June 11–15, 1947 (Öld Greby Alvar[†]).

N. reitteri. Lyl Tärna, Yttervik, mixed forest (440 msl), August 23, 1945, 1 specimen; Gejmån, June 20–21, 1948, 3 specimens, all in *Regio coniferina* (FRD).—Tol Tjårro (north of Nedre-Soppero), June 17, 1948, 1 specimen (HLD!).—24 Dovre, Kongsvoll, 1920, 1 specimen (LYS, MD!). 30 Unkersvatn, July 2, 1947, 1 specimen (FRD).

H. rufipes. Skå Börringekloster, November 1, 1923, 1 specimen (KMN; NYH, O. E., 1945, p. 153; ML).

Odacantha melanura. Gtl Fårön, Ava, sea drift, June 16–17, 1946 (Palm). Upl Älvkarleby, Gärdskär, seashore, 1942, several specimens (ELS).—Sv Gumbaritsa, Ladoga shore, June 1942, 1 specimen (PME, 1946, p. 42!). Ösel (SZL, 1942, p. 186).

In Denmark oviposition in mid-May, larvae half-grown at the end of June (West, 1941, p. 632).

In Holland there is a report of flight (Tijdschr. v. Ent., 70, 1927, p. XII) that was not taken into consideration above.

Olisthopus rotundatus. "8 Vadheim" (KLF) should be excluded, since it actually pertains to *O. synuchus*!—Al Sottunga, 1943, 1 specimen (LBÅ). Kl Harlu, 1 specimen (PME!).

In captivity likes to feed on bread (Ögl).—The flight capacity of the

[†](Plant community consisting typically of mosses and calciphilous herbaceous plants that grow on steppelike shallow alkaline soils overlying Scandinavian limestones; suppl. scient. edit.).

macropterous form was established by the discovery of one macropterous specimen "on *Sphagnum acutifolium* quaking land" near Ab Sammatti, 925 (KRG!).

Omophron limbatum. Ble Jämjö, July 28, 1945, several specimens (SDH!); Torhamn, Färsksjön, September 26, 1947, several specimens (BRK).

Oodes gracilis. Sdm Öster-Malma, June 1946, 1 specimen (HLD!). The frequency of the species at Upl Ösbysjön is evident from the fact that at the small sampling plot I (LTH, 1943a) 50 specimens were collected in 1 1/2 hours on June 3, 1947.

In spring 1947 near Upl Ösbysjön, appearing as early as May 7 (3 specimens) after an unusually hot day (Matthiessen).—The beetle likes to feed on bread.

O. helopioides. Gst Mårdängsjon, May 29, 1947, 8 specimens (LBL, RM!). —Ösel (SZL, 1942, p. 182).

In contrast with *O. gracilis, O. helopioides* is not a definite migrant. More than 10 specimens were found on April 22, 1945, right at the edge of "Norrakårr," Upl Danderyd, among moss and in turf, apparently at the place of hibernation (LTH). In Sv hibernating under *Salix* foliage close to the shore (PME, 1946, p. 30).

Panagaeus bipustulatus. Ögl Mogata, together with *Brachynus*; larva August 14, adult August 17, 1946 (LTH).—Kl Salmi, June 23, 1944, 1 specimen (PME!).

The beetle likes to feed on bread (Öld).

P. crux-major. Ble Jämjö, Färsksjön, July 28, 1945 (SDH!). Upl Älvkarleby, Östana, June 22, Hyttön, July 1, 1945 (ELS!). Hls Bergvik, December 30, 1944, 3 specimens (HLD!).—Ösel (SZL, 1942, p. 183).

Patrobus assimilis. Oa Lappfjärd, 1944 (LBÅ).—Latvia, Tauerkaln, 1938, 1 specimen (LCK, 1942, p. 173).—Pechora region, Pjoscha River and Kuloj River (KLM, MH!). Northern Ural, Kondinsk (BGR, according to SBJ, 1880, p. 21; MH!).

In Sv immature beetle, August 13 (PME, 1946, p. 29).

P. atrorufus. Vbt Hällnäs, July 25, 1947, 2 specimens (HEQ!). Lyl Skalmodal, June 24–28, 1947, several specimens (as far as 540 msl, *Regio betulina*) (FRD!); Strimasund (525 msl), July 18, 1946, 1 specimen (FRD!).—Om Haapavesi (Arppe, coll. Y. Kangas!).

P. septentrionis. 8 Gloppen, Gjengalundsbraeen (1000 msl), August 9, 1946, 2 specimens, (WSJ!).

867 Near Lyl Tärna, Rufjället, as far as 1400 msl, August 22, 1945 (FRD). —Interglacial fossil record on Iceland (Thorkelsson, 1935, p. 5).

P. septentrionis australis. Sb Vehmersalmi (HDL!).—In Sjaelland 2 new localities (West, 1947, p. 11).

Pelophila borealis. Vbt Vännäs, July 7, 1944 (SDH!)

In Lyl Tärna region (northern Storfjället, Stropiålke) as far as 1040 msl, August 6, 1945 (FRD).

Perigona nigriceps Dej.*

Sweden. 1 specimen of this cosmopolitan species was collected by S. Berdén on July 17, 1948, in a park near Skå Alnarp in the evening by sweeping (O. E., 13, 1948, p. 167!).

Not known elsewhere in Fennoscandia or neighboring regions.

Total Area: The species originates from the environs of the Indian Ocean (JEA, 1941–42, p. 581), but was transported with traffic to West Africa, North and Central America, as well as displaced to Europe. Northward only as far as Moravia and Rhineland (HOR, 1941, p. 190); later there are several records northward as far as Lübeck (Kol. *zeitschr*., 1, Frankfurt, 1949, p. 83). Perhaps the Swedish record is the forerunner of an impending invasion.

Ecology

The insect lives in compost and all kinds of modern herbs, partly subterranean.

Biology

I know nothing about the development periods and the feeding habits.

Dynamics

The wings are well developed, and the species has been repeatedly observed in flight, especially in the evening (JEA, l.c.).

Pristonychus terricola. Ab Korpo, June 12, 1944, 1 specimen (WEG). Nl Helsinki, 3 specimens in a cellar, April 1949 (LBG).—Ösel (SZL, 1942, p. 185).

Pterostichus adstrictus. In Lyl Tärna region as far as 680 msl (*Regio betulina*), 1945 (FRD).

P. angustatus. From Sv no association of the species with burned wood is reported by PME (1946, pp. 36–37) but he regards it as "a very characteristic species of boggy spruce and pine forests," which has also been found on drier soil.—Immature beetles, August 20–22, 1942, found in large quantities (Sv; PME, l.c.).

P. anthracinus. Gtl Sandön, June 28, 1947 (WRN!).

In connection with crossing experiments (LTH, 1946) some observations were made on the development periods (under optimal conditions, at room
868 temperature): copulation, April 16 through May 22; oviposition, May 12 through June 1; larvae hatching from May 19 through June 9; first molt,

*Since *Perigona nigriceps* occurs only accidentally in our region it has been ignored in calculating the different percentages of the carabid fauna of Fennoscandia as a whole.

May 28 through June 19; second molt, June 5 through July 7; pupation June 26 through July 12; emergence of adults, July 4 through 17. The shortest total period of development from oviposition to emergence of the adult was 9 + 9 + 8 + 12 + 7 days = 45 days. Found near Öld Halltorp under moss of fallen, decaying, wet oak trunks in very shady location on June 11, 1946: one pair in copulation, numerous females with eggs in their cavities, and two batches of freshly hatched larvae.—In captivity the beetle feeds on bread but prefers animal food; the larvae were fed exclusively with fresh pieces of *Lumbricus*.—A reared specimen flew in the evening during artificial light. 2 specimens flying to light in Hungary (Dorn, 1946).

P. aterrimus. Öld Högsrum, Gladvattnet, June 20, 1947, 1 specimen (LBL!).

P. coerulescens. Copulation on June 10, 1947 (Skå Hälsingborg, PLQ).—In captivity the larva was partly cannibalistic (LNG, 1921, p. 76).

P. cupreus. Oa Lappfjärd, 1944 (LBH). Kl Valamo (Y. Kangas).

Spontaneous flight during sunshine, May 14, 1948, 2.00 p.m. (Stockholm, LTH).

P. diligens. Interglacial fossil record on Iceland (Thorkelsson, 1935, p. 5).

P. gracilis. Gtl Sandön, June 30, 1947, 1 specimen (WRN!).—Al Eckerö, Torp, 1943, 1 specimen (LBA). Ta Tavastehus, May 1940 (NUM).

P. lepidus. Sdm Mörkö (Ekstrom, 1828, p. 50). Upl Adelsö, May 25, 1947, 1 specimen (LTH); Roslags-Näsby, 1943 (OLS!). Lyl Umgransele, numerous (B. Persson!).—30 Grong (LYS, MD!).—Record specimen on Lm Kantalaks in MH (!).

Copulation on August 22 (Sv; PME, 1946, p. 36), in captivity on August 11 (Nl Tvärminne, LTH).—In captivity likes to feed on bread (Nl).

P. minor. On the British Isles, too, the species shows wing dimorphism, with about the same ratio of the two forms (Sharp, 1913).

P. niger. Dlr Bingsjö, 1945 (F. Månsson, according to KLF).

In Central Europe apparently dimorphic (Maran, 1927). On the British Isles the species may be constantly macropterous, as in our region, but according to Sharp (1913) not all specimens are capable of flight. Spontaneous flight of 1 specimen to light near Temesvár in Hungary (Dorn, 1946).

P. nigrita. North Africa (SZM, *Atti Soc. Ital. Sci. Nat.*, 80, 1941, p. 61).

On Gäutavardo near Lyl Tärna, 1 specimen in the lower *Regio alpina* (825 msl), June 23, 1945 (FRD!).—Spontaneous flight (during sunshine); Skå Silvåkra, April 20, 1947 (CHR); Upl Danderyd, Nora, May 13, 1945 (LTH); Ängby, May 27, 1946, 3 specimens (LTH).

P. oblongopunctatus. Distribution map in HNR (1933, p. 308).—Skå St Oloi, May 23, 1945, 1 specimen (HEQ!). In Lyl Tärna region as far as the lower *Regio betulina* (550 msl) (FRD!).

P. punctulatus. The locality Skå Ystad (Palm) should be deleted.

P. strenuus. Spontaneous flight of 1 specimen during sunshine near Sb Vehmersalmi, June 1946 (HDL!).

P. vernalis. 16 Bandak (MST, MO!).—Ka Virolahti (PFF, MH!). Oa Lappfjärd, 1944 (LBH); Vasa (Kontuniemi!). Ob Hailuoto (WUO, 2 specimens, MH!).—Kn Kontupohja (Vaartaja, MH!).

The considerable variability of wing size was noted by Sharp for the British Isles (1913, p. 86).

P. vulgaris. Hls Ramsjö (LDN).—Kr Kontschosero (SBJ, MH!); Suma (LEV, MH!). Late glacial fossil record from Ireland (Jessen and Farrington, 1938, p. 241).

869 *Sphodrus leucopthalmus*. Sb Vehmersalmi, 2 specimens under the floorboards of a flour warehouse, 1946 (HDL).

Stenolophus mixtus. Öld, southern end of Möckelmossen, June 15, 1947, 1 specimen (LTH). Gtl Östergarn, Sandviken, on the seashore, June 6, 1948, 1 specimen (WSJ!)*.—Ta Kuusankoski, Voikka, July 1947, 1 specimen (NUM).

In Sv numerous beetles as early as June and July (PME, 1946, p. 31).

Stomis pumicatus. Dlr Leksand, Leksandsnoret, June 1948 (G. Enlund, according to KLF).

Synuchus nivalis. 8 Vadheim, August 11, 1937 (KLF!).—Ösel (SZL, 1942, p. 185).

Tachys bisulcatus. Skå Lomma, 1 specimen on the wall of a house, June 13, 1947 (S. Berdén!). Små Överum, July 7, 1945, June 10, 1946, numerous specimens (JNS, E. T., 1947, p. 4). Vrm Lundsberg, 1945, 2 specimens, flying in the evening (WRN).

Tachyta nana. Hls Bergvik, May 3, 1947 (HLD!).

Observed repeatedly feeding on Collembola (Sv; PME, 1946, p. 28).

Tachypachys zetterstedti. Sv Olonets (PME, 1946, p. 20).

In Sv found on bog soil or in boggy mixed and coniferous forests, altogether 6 specimens; thus probably a hygrophilous species (PME, l.c.).

Trechus discus. Vrm Lungsund, Kungsskogen, July 23, 1947, 1 specimen (WRN); Varpnäs, August 1947, flying specimens (OSS!). Hls Los, August 7, 1947, flying specimens (SJB).—Sa Villmanstrand, 1942 (HDL).—Also in northern Jutland (West, 1947, p. 11).

HOR (*in litt.*) does not assume any association of this species with animal nests. Immature beetle, June 5 (southern Germany, HOR, *in litt.*).

T. fulvus. 6 Sande, May 24, 1928; Sandebukten, May 2, 1933; Hafsjord, May 17, 1942; each time only 1 specimen, always right at the seawater (JEN).

T. micros. Svir region without specific locality data, 1944 (PME, 1946, p. 28).

T. obtusus. Lyl Tärnaby, Abelvattensdal and Vapsdal, several localities also in *Regio betulina* (as far as 750 msl), 1946, 1947 (FRD).—8 Gloppen, Skjerdal, August 1946, 2 specimens (WSJ!).

In Hjd (Hamrafjäll), also collected by FRD in the lower *Regio alpina* next

*This record was not considered in the treatment of the fauna of the islands.

to a snowdrift, July 1944.—Immature beetle, August 18–20 (8 Gloppen, WSJ!).

T. quadristriatus. Vrm Torsby, Sörbo, August 10, 1944 (SVS).—Om Nedervetil, 1943 (LBÅ).

T. rivularis. Upl Fiby, September 1947 (LBL).

T. rubens. Lyl Tärna region, 2 localities, 1945, 1946 (FRD).

T. secalis. The locality Hls Los (SJB) should be excluded.—Ösel (SZL, 1942, p. 193).

In Sv the beetle appears around July 1, but immature specimens are observed as late as in August (PME, 1946, p. 28).

Trichocellus cognatus. Vgl Gårdsjö, June 30, 1942, 2 specimens (BRC!). Lyl Tärna region, 2 localities (as far as *Regio betulina*), 1946 (FRD).—Oa Lappfjärd, 1944 (LBH).—Denmark, southern Fyen (West, 1947, p. 14).

T. placidus. Gtl Fårön, Ekeviken, sea drift, May 9, 1948, 2 specimens (HLD!). Hls Ramsjö (LDN). Oa Lappfjärd, 1944 (LBH). The locality Lk Muonio is doubtful.

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902–911 Only the carabids found in Fennoscandia, Recent or fossil, are included here. There is no reference to entries in the Supplement (p. 843).

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